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REMARKS ON THE POSITION, THE DELIMITATION AND THE SUBDIVISION OF THE RUBIACEAE

C. E. B. BREMEKAMP

(Botanical Museum and Herbarium, Utrecht)

(received October 22nd, 1965)

INTRODUCTION

It is often assumed that the delimitation and the subdivision of the various families which have been distinguished in the Angiosperms, do no longer offer serious difficulties. They would belong to those objects of study for which already long ago a fairly satisfactory solution was found. If we wish to be acquainted with this solution, the only thing we would have to do, would be to look up such works as Bentham and Hooker's "Genera Plantarum" and Engler and Prantl's "Natürliche Pflanzenfamilien". Some improvements might still be desirable, but these would be of minor importance only. These assumptions, however, are to be regarded as dangerous illusions.

That the very serious nature of the shortcomings found in the delimitation and subdivision of these families, especially of the larger ones, is so often overlooked, is apparently due to an attitude of mind which is observed in a comparatively large part of the taxonomists, viz. a lack of interest in the development of a truly natural classification. This is not incomprehensible. Most of them spend the major part of their time in the elaboration of floras covering areas of more or less limited extent, and they are but rarely aware of the fact that the knowledge of the families which is obtained in this way, remains necessarily incomplete. Moreover, in the elaboration of a flora the most essential point is the construction of serviceable keys to the species as well as to the groups of higher rank, not the exact delimitation of these groups: to the latter end usually more material is required than the compiler of a flora has at his disposition. However, we must not overlook the fact that a key, in order to be serviceable, need not reflect the degree of affinity between the units with which it is dealing; in reality, such keys are often entirely or almost entirely artificial, and this applies therefore also to classifications which are based on such keys. To illustrate this, I will discuss here some of the characters by the aid of which in the *Rubiaceae* very suitable keys to the genera have been constructed, but which when they subsequently were used for the elaboration of a classification, led to entirely unsatisfactory results.

To the characters which for a long time have played an important part in the subdivision of the *Rubiaceae*, belong the presence either of uni- or of pluriovular ovary cells, their kind of fruits, which to this end were divided in dry and fleshy ones, and the nature of their seeds, of which also two kinds were distinguished, viz. winged and wingless ones. However, even a superficial study of the groups that have been distinguished by the aid of these characters, will show that most of them are entirely unnatural. As the differences are morphologically of hardly any value, this might have been expected.

The number of ovules per ovary cell shows a continuous range of variation, and so long as there is no reason to assume a correlation between a definite number of ovules and one or more other characters, it is therefore not justified to attach to the presence of one or two ovules per ovary cell a greater taxonomic value than to that of three or of another number of them; we know, in fact, that the number of ovules per ovary cell may vary within the limits of a single genus (see my "Monograph of the genus *Pavetta* L" in Fedde, Repertorium **37**: 10. 1943, and my remarks on the genus *Anotis* DC and the *Cruckshanksieae* in the last chapter of the present publication) as well as in genera that on account of their many common features are to be regarded as nearly related, so e.g. in *Tarenna* Gaertn. and *Pavetta* L (see p. 7 of my "Monograph of the genus *Pavetta* L").

That the difference between dry fruits and fleshy ones can not be used for the characterization of natural groups is also easily comprehensible. This distinction is an ecological, not a morphological one, and in both kinds of fruits quite considerable morphological differences are found; in some instances the differences between a dry and a fleshy fruit may even be smaller than those between two kinds of dry fruits or two kinds of fleshy ones. In the genus *Mussaenda* L species with dry fruits are found side by side with species producing fleshy ones; even if these species are divided over two genera, as sometimes is done, this does not make much difference, for in that case we will have to admit that the two kinds of fruits are found in very nearly related genera.

The same applies to the distinction between winged and wingless seeds: this too is an ecological, not a morphological distinction. From the morphological point of view these wings are by no means all alike; in the *Cinchoneae*, the tribe in which the genera with winged seeds were brought together, they are in the genera which may rightly be regarded as near allies of *Cinchona* L, in position as well as in the structure of the cells of which they are mainly composed, entirely different from those that are found in the genera which were transferred by me to the *Rubioideae*.

Another drawback of the classifications accepted in the works mentioned above, is that they are based mainly on earlier classifications which were drawn up when a much smaller number of genera were known, and that the authors often assumed that the subfamilies and even the tribes based on this more limited number would suffice for the incorporation of the subsequently discovered genera. This apparently is the explanation of the fact that so often a genus has been squeezed into a tribe into which it does not fit. In the case of the *Rubiaceae* there are even quite a number of genera of which it is extremely doubtful whether they really belong to this family. This point will be discussed in the second chapter.

Many taxonomists, moreover, seem to feel a certain reluctance to accept subfamilies which contain but a single tribe, and tribes which contain but a single genus. This reluctance, however, is entirely unjustified. We know several families and even some orders which contain but a single or a very small number of genera, and there is accordingly no reason whatever for assuming that a subfamily or a tribe should always contain more than one group of the next lower rank. Whether a taxon is to be classified as a subfamily or a tribe evidently depends upon the number and the importance of the characters in which it differs from its nearest allies and on nothing else, and where our predecessors have overlooked the presence of some differences or undervalued their importance, it is doubtless our duty to correct them.

With regard to what has been said in the preceding paragraph, it is, of course, of importance to find ways and means for estimating the taxonomic value of the groups of characters that are to be used for the distinction of the tribes and subfamilies and, naturally, of the families too. In the case of the latter the number of diagnostic characters is often extremely small and their value not rarely dubious. With regard to the *Rubiaceae* this point will be dealt with in the chapters one and two, but at this point it is perhaps worth while to draw the attention to the fact that in the description of this family given in the works mentioned above we do not find a single character that can be regarded as a truly general one. This is, of course, due to the fact that this family, in the delimitation accepted in these works, comprises elements which do not really belong to it. The inclusion of such elements, moreover, has often led to entirely false conclusions with regard to the affinity of the families. In the case of the *Rubiaceae*, for instance, the inclusion of the genera *Henriquezia* Spruce ex Bth. and *Platycarpum* Humb. et Bonpl. has led to the assumption that there should be a comparatively close affinity between this family and the *Bignoniaceae*. However, when these two genera are excluded, it appears that not a single argument is left which might possibly be adduced in favour of this view. After the exclusion of the genera *Carlemannia* Bth. and *Sylvianthus* Hook. f. the affinity with the *Caprifoliaceae* and their allies has become less pronounced, and if the genus *Dialypetalanthus* Kuhlm. had been left in the *Rubiaceae*, this would have been a good argument for assuming a rather close affinity with the *Myrtales*! It is therefore of great importance that such misclassifications are corrected. Several other examples of genera which were incorporated in the *Rubiaceae* on insufficients ground, will be given in the chapter dealing with the delimitation of the family.

It can, of course, not be denied that the number of characters which related taxa have in common, decreases with the increase in rank of the taxon to which they belong; it is certainly no wonder that families have, as a rule, but a very small number of general characters. However, groups based on a single general character should always be regarded with some distrust.

Verdcourt (Bull. Jard. bot. de l'État, Bruxelles **28**: 228. 1958) discusses my subfamily *Ixoroideae* and rejects it because the pollination mechanism which is a general feature of this group, is thought to be present also in some genera which belong to other circles of affinity, a point that will be discussed in chapter three, and further because this pollination mechanism is regarded by him as a single character. This is certainly not so. The type of pollination mechanism which is characteristic for the *Ixoroideae* requires that the anthers are in the bud in contact with the part of the style which serves as a temporary depository for the pollen grains; this means that they must be found at the same height as the latter and that they open introrsely. The part of the style which serves as "*receptaculum pollinis*" must be covered with short hairs, otherwise it would be unable to fulfil its function. Finally the flowers must be protandrous. This type of pollination mechanism is therefore a much more complex arrangement and accordingly of much greater taxonomic importance than most other pollination mechanisms, e.g. than the heterostylism to which Verdcourt himself attaches a relatively high value. As I have discussed some time ago the relatively small taxonomic value of this kind of pollination mechanism in my paper "On pollen dimorphism in heterostylous *Psychotrieae*, especially in the genus *Mapouria* Aubl." (Grana palynologica **4**: 54 and 55, 1963) it seems superfluous to enter into details. Suffice it to state that heterostylism is found in several but distantly related families, that it is always restricted to part of the genera and that it is even in these genera but rarely a general feature. With the kind of pollination mechanism found in my subfamily *Ixoroideae* this is quite different. It is apparently restricted to this subfamily of the *Rubiaceae* and to a few other families, viz. the *Campanulaceae*, the *Goodeniaceae* and the *Compositae*, and in the two last-mentioned families the mechanism is not even quite the same, for the hairs on the style have here a different function; moreover, the receptaculum pollinis of the *Goodeniaceae* (the "Pollenbecher" of Schönland) occupies a different position and shows a different structure, whereas in the *Compositae* the receptaculum pollinis is lacking. In contradistinction with heterostylism this kind of pollination mechanism and its variations are in all the groups in which they occur, a fully general feature. The combination of characters on which it rests, is therefore to be regarded as taxonomically highly important.

My subfamily *Rubioideae* was accepted by Verdcourt l.c. as a natural one, although the tribes which at that moment were united in this group, had but one character in common, viz. the presence of raphides. I may add here that one of the two other subfamilies recognized by Verdcourt, viz. the *Cinchonoideae*, has in the delimitation accepted by him not a single general character, for the absence of raphides can certainly not be regarded as such; this would be possible only if it could be proved that they possess some mechanism which prevents the development of this kind of crytals, and that this mechanism moreover, is the same in all the tribes that have been included in this subfamily.

That the presence of raphides is to be regarded as a taxonomically very important feature, follows from the fact that it is in the tribes in which it occurs, a general character, whereas this kind of crystals is completely absent in the other tribes of the *Rubiaceae* and also in all the families which are to be regarded as their nearest allies. In itself, however, their presence is not sufficient to prove that the affinity of the tribes in which they occur, is so close that they are to be united in a single subfamily. In this connection it is noteworthy that most of these tribes agree also in another character, viz. in the valvate aestivation of the corolla lobes. There are, however, two tribes in which another kind of aestivation of the corolla lobes is found, viz. the *Hamelieae*, where the aestivation is imbricate, and the *Hillieae*, where it is contorted. The inclusion of the *Hamelieae* in the *Rubioideae* is perhaps permitted, as at least in one of the tribes in which the aestivation is said to be valvate, viz. the *Psychotrieae*, at least two genera are included, viz. *Notopleura* Brem. and *Naletonia* Brem., in which the aestivation is imbricate. These two genera, of which the first was regarded by Hooker as a section of *Psychotria* L, are in all other respects normal members of the tribe *Psychotrieae* (see my "Notes on the *Rubiaceae* of Surinam" in Rec. d. trav. bot. Néerl. **31**: 284 and 289. 1934). The case of the *Hillieae*, however, is an entirely different one. The inclusion of the genus *Hillia* Jacq. in the *Cinchoneae* was made possible by Hooker by means of a slight change in the definition of the latter; according to him the seeds of the *Cinchoneae* would be "alate or appendiculate", but the word "appendiculate" has obviously been added with the sole purpose of legitimizing the inclusion of this genus, but this can not be regarded as an acceptable solution of the difficulty caused by the neccessity of finding a place for this aberrant genus, for the tuft of hairs at the top of the seed can certainly not be homologized with a wing. That the wings with which the seeds in the other genera which by Hooker, and at an earlier date already by de Candolle, were included in this tribe, would prove to be of different kinds, could not be foreseen at that time, but this excuse can not be brought forward in the case of the genus *Hillia*, as the latter does not show the slightest resemblance to any of the genera with winged seeds that rightly or wrongly were brought together in this tribe. Schumann makes it even worse, for notwithstanding the fact that according to his definition of the *Chinchoneae* the seeds are always winged, he too includes the genus *Hillia* in this tribe. *Hillia*, however, occupies a very isolated position in the family. One of its most remarkable features is found in the structure of the testa cells, which show a rather striking resemblance with those of the genus *Gleasonia* Standl., another genus occupying a rather isolated position; in their other characters, however, these two genera show no resemblance whatever. *Hillia* as well as *Gleasonia* are therefore referred by me to subfamilies of their own.

I. THE POSITION OF THE RUBIACEAE

In order to determine the taxonomic value of the various characters that are met with in a family, it is desirable to know something of the distribution of these characters in the families which are to be regarded as its nearest allies. With this end in view we will consider briefly the position which is to be assigned to the *Rubiaceae* in the system of the Angiosperms. In more recent times this problem has been discussed at some length by UTZSCHNEIDER (Mitt. Bot. Staatssamml. München **3**: 96-98. 1951) and by WAGENITZ (Bot. Jahrb. **79**: 17–35. 1959).

Wagenitz comes to the conclusion that the order of the *Rubiales* as defined in Engler's "Syllabus", i.e. as a group comprising the *Rubiaceae*, *Caprifoliaceae*, *Adoxaceae*, *Valerianaceae* and *Dipsaceae*, can not be regarded as a natural one, because the points of resemblance between the *Rubiaceae* and the other families included in this group appear to be of less importance than those between the *Rubiaceae* and some of the families that were included in the order which at that time was known as the *Contortae*. These points of resemblance become even more striking if this order is given a more natural delimitation by removing the *Oleaceae* to an order of its own, the *Oleales*, and the *Buddleiaceae* to the order formerly known as the *Tubiflorae*, where it may be put in the vicinity of the *Scrophulariaceae*, a family in which some of its representatives formerly had been included, e.g. by de Jussieu. On account of the many points of resemblance which the *Rubiaceae* show with the *Loganiaceae* and their nearest allies, they are included by Wagenitz in this group of families, for which he introduces the name *Gentianales* Lindley emend. Wagenitz. This order, therefore, comprises in his delimitation the families *Loganiaceae*, from which the *Buddleioideae* are excluded, *Rubiaceae*, *Apocynaceae*, *Asclepiadaceae*, *Gentianaceae* and the rather aberrant *Menyanthaceae*. The other families of the former *Rubiales* are kept together in an order for which he uses the name *Dipsacales* Lindley emend. Nakai.

The points in which the *Rubiaceae* resemble the other families of the *Gentianales* sensu Wagenitz and those in which they differ from the *Dipsacales* sensu Nakai may be summarized as follows. The leaves of the *Gentianales* are, except in the *Menyanthaceae*, decussate or, more rarely, verticillate, those of the *Dipsacales* either decussate or alternate; in the *Gentianales* they are, moreover, simple and entire, though here too an exception to this rule is found in the *Menyanthaceae*, whereas in the *Dipsacales* they are either simple or, more rarely, pinnately compound and often dentate or more deeply incised. The corolla is in the *Gentianales* always actinomorphic, and in the *Dipsacales* either actinomorphic or, more often, more or less distinctly zygomorphic. The androecium is in the *Gentianales* always isomerous, in the *Dipsacales* either isomerous or oligomerous. The endosperm is, as far as can be judged at present, in the *Gentianales* always nuclear, in the *Dipsacales* always cellular. The stipules are in the *Gentianales* often provided with colleters, whereas these appendages of the stipules are in the *Dipsacales* always absent. True glandular hairs are, on the other hand, but rarely met with in the *Gentianales*, whereas they are of common occurrence in the *Dipsacales*. Another point of similarity between the *Rubiaceae* and the other families of the *Gentianales* may perhaps be seen in the presence of alcaloids; in the *Dipsacales* these substances are absent or at least very rare. Alcaloids belonging to the group of the tryptophans seem to be confined to the *Loganiaceae*, the *Apocynaceae* and the *Rubiaceae*. However, as they are not found in all the genera belonging to these families, their presence would only be of importance to the taxonomist if it could be proved that they are derived from precursors which are generally present in the *Gentianales* and absent in the *Dipsacales*. So far the most important points of resemblance between the *Rubiaceae* and the other families of the *Gentianales* seem to be the presence of colleters and the nuclear endosperm, the most important difference the absence of intraxylary phloem in the *Rubiaceae* and its presence in the other families, and the position of the ovary, which in the *Rubiaceae* is inferior or at least more or less so, and in the *Gentianales* always superior. In these two points the Rubiaceae agree with the *Dipsacales*.

The taxonomic importance of the inferior ovary, however, should not be overrated. In the great majority of the *Rubiaceae* the ovary is indeed completely inferior, but in the *Gaertnereae*, a tribe of the *Rubioideae* nearly related to the *Psychotrieae*, the ovary, though at first still partly inferior, becomes in the later stages of its development almost completely superior, and in some genera belonging to other tribes the proportion between the part of the ovary which rises above the place of insertion of calyx and corolla and that below the latter, may vary considerably. In the genus *Mitrasacmopsis* Jovet, which by its author was included in the *Loganiaceae-Spigelieae*, the ovary is, as in the *Gaertnereae*, almost completely superior; the presence of raphides proves that this genus can not belong to the *Loganiaceae*, a family in which raphides are entirely unknown, but that it is to be transferred to the *Hedyotideae*, a tribe of the *Rubioideae*; it is, in fact, a near ally of my genus *Diotocranus*, in which the ovary is also almost completely superior; the two genera even may prove to be identical.

Another point which deserves our attention when we wish to estimate the taxonomic value of the inferior ovary, is that ovaries of this kind are found in widely different families, and that in some of these families, e.g. in the otherwise rather uniform *Gesneriaceae*, superior as well as inferior ovaries are met with. The example of the *Gesneriaceae* is the more instructive as this family belongs to the *Tubiflorae*, an order in which all the other families are provided with superior ovaries.

The considerations expounded in the two preceding paragraphs lead to the conclusion that in the *Rubiaceae* the presence of an inferior ovary can be regarded only with some reserve as a general character, and that this character, moreover, is not of so paramount importance that it would in itself be sufficient to exclude this family from the *Gentianales* and to compel us to regard it as more nearly related to the *Dipsacales*.

The absence of an intraxylary phloem in the *Rubiaceae* forms doubtless a more serious obstacle against the inclusion of this family in the *Gentianales*, as this is a character which is less irregularly distributed.

Considered in connection with the admittedly less important inferior ovary it would perhaps justify the creation of a monotypic order *Rubiales*. The latter would, however, be more closely related to the families which would be left in the *Gentianales* than to the *Caprifoliaceae* and the other families of the *Dipsacales*.

Apart from the affinity with the *Gentianales* and the *Dipsacales* that with the *Campanulales* should also be considered. In this connection the resemblance between the pollination mechanism of the *Ixoroideae* and that found in the *Campanulaceae*, the *Goodeniaceae* and the *Compositae*, which was discussed in the introduction, would perhaps deserve more attention than it has received so far.

II. The delimitation of the Rubiaceae

In the introduction to this paper we have already pointed out that the genus *Dialypetalanthus* Kuhlm. had to be excluded from the *Rubiaceae* because it shows in the structure of the flowers with their polymerous androecium an unmistakable affinity with the families brought together in the *Myrtales*. We might have added that nowhere else in the *Rubiaceae* any indications of an affinity with this order is to be found (cf. Rizini et Occhioni in Lilloa **17**: 253. 1949). For a similar reason *Henriquezia* Spruce ex Bth. and *Platycarpum* Humb. et Bonpl. had to be excluded. These two genera show in the slightly zygomorphic corolla and in the quite distinctly zygomorphic androecium and also in the large exalbuminous seeds a high degree of similarity with the *Bignoniaceae* and some other families of the *Tubiflorae*, whereas elsewhere in the *Rubiaceae*, if we except a few other anomalous genera which, as I will show hereafter, have been included on insufficient grounds, no indications of such a relationship can be detected (see my paper "On the position of *Platycarpum* Humb. et Bonpl., *Henriquezia* Spruce ex Bth. and *Gleasonia* Standl. in Acta Bot. Neerl. **6**: 351 377. 1957). The genera *Carlemannia* Bth. and *Sylvianthus* Hook. f. were excluded already at a much earlier date by Solereder (Bull. Herb. Boiss. **1**: 173–178. 1893). On account of the dentate or serrate leaves, the rudimentary stipules and the oligomerous androecium they are to be removed to a position in the vicinity of the *Caprifoliaceae*, i.e. to the *Dipsacales* (see my note on these genera in Rec. d. trav. bot. néerl. **36**: 372. 1939).

The genera mentioned above are not the only ones that will have to be excluded, whereas the position of some other genera is extremely doubtful and should be reconsidered.

The genus *Opercularia* Gaertn., now usually included in the *Anthospermeae*, was on account of its unilocular ovary and the oligomerous androecium referred by de Jussieu (Ann. Mus. d'Hist. Nat. **4**: 118. 1824) to a family of its own, the *Operculariaceae*, but Richard (Mém. sur la famille des Rubiacées: 62–67. 1830), who distinguished in this group of species two genera, viz. *Opercularia* Gaertn. and *Pomax* Soland. ex A. Rich., included it as a separate tribe in the *Rubiaceae*, and this example was followed by de Candolle in his "Prodromus". Richard rejected the decision taken by de Jussieu, because in his opinion the number of stamens would vary in the *Rubiaceae* and because in that family more examples of genera with unilocular ovaries would occur. Richard, however, was mistaken, for in the genera which on good grounds have been referred to this family the androecium is always isomerous and the ovary is always divided in two or more cells. Exceptions to this rule are found in the genus *Eleutheranthus* F. v. Müll., which is doubtless a near ally of the genera *Opercularia* and *Pomax*, in the genus *Tammsia* Karst., which will be discussed hereafter, and in some genera which have been included in the *Gardenieae*, viz. in the type genus *Gardenia* Ellis and the nearly related genera *Macrosphyra* Hook, f. and *Casasia* A. Rich., and also in *Villaria* Rolfe. However, as RICHARD (op. cit. 214–215) already pointed out, the structures on which in these genera the ovules are inserted, though distinctly separated from each other in the basal part of the ovary, are in the upper part not rarely united; for this reason they can very well be regarded as dissepiments, in which case the ovary would have to be described as imperfectly 2- or more-locular. The genera *Opercularia, Pomax and Eleutheranthus* ought certainly to be studied in more detail; I expect that such a study will confirm the standpoint of de Jussieu, and that as a further result his family *Opercularіaceae* will prove to belong to the *Dipsacales*.

Other genera of doubtful position are *Tammsia* Karst., *Pentagonia* Bth., *Hippotis* Ruiz et Pav. and *Sommera* Schlecht. These four genera were regarded by SCHUMANN (Natürl. Pflanzenfam. IV, **4**: 69. 1891) as nearly related because of the peculiar striation of their leaves. This so-called moiré or watered striation, however, is not restricted to these genera, but is found also in the Malesian species of the genus *Antirhea* Commerc. (see my paper on a South-American species of this genus in Acta Bot. Neerl. **8**: 480. 1959), and as to the four genera mentioned in the preceding sentence, it is by no means certain that they may be regarded as nearly related. The genus *Tammsia* with its unilocular ovary and parietal placentas differs considerably from the three other ones; in combination with the anisomerism between calyx and corolla and the zygomorphism of the latter and of the androecium, these characters make the position of this genus in the *Rubiaceae* extremely doubtful. Of one of the species of *Pentagonia* it is said that it has pinnatifid leaves; this too is a character which is never met in the genera which on good grounds have been included in this family, and if this species has correctly been referred to this genus, the latter will doubtless have to be referred to another family. *Hippotis* and *Sommera* are less aberrant. The strongly zygomorphic calyx and the less strongly, although still distinctly zygomorphic corolla found in *Hippotis*, a combination of characters which by RICHARD (op. cit.: 176) was compared with that met with in the genus *Spathodea* P. Beauv. (*Bignoniaceae*), are doubtless unusual features, but they would in themselves not suffice to exclude this genus from the *Rubiaceae*, and *Sommera* seems to fit even better in this family. However, before a final decision can be taken, these four genera should be studied in more detail.

The genus *Aitchisonia* Hemsl., for which a place has been found in the *Paederieae*, though on what grounds is not clear, is, on account of the insertion of the stamens at various heights in the corolla tube and of the presence of glandular hairs, certainly to be excluded from this family. As I have pointed out on p. 153 of my "Monographie des genres *Cremocarpon* Boiv. ex Baill. et *Pyragra* Brem." (Candollea **16**: 147–177. 1958), the combination of raphides and glandular hairs which is found in this genus, is vary rare and does not occur in any other genus provided with interpetiolar stipules and a bilocular ovary with a single ascending ovule in each of the cells. For this reason we will have to assume that *Aitchisonia* represents an as yet undescribed family, which probably will have to be put in the *Dipsacales* in the vicinity of the *Caprifoliaceae*.

The genera *Gaertnera* Lam. and *Pagamea* Aubl. were originally included in the *Loganiaceae*, but were transferred by Baillon and Schumann to the *Rubiaceae*, where they were placed, on account of the solitary ascending ovules and the valvate aestivation of the corolla lobes, in the *Psychotrieae*. In my "Notes on the *Rubiaceae* of Surinam" (Rec. d. trav. bot. néerl. **31**: 248. 1934) I returned them to the *Loganiaceae*, but in my communication to the 8th Botanical Congress held in Paris, of which an abstract was published on p. 113 of the "Rapports et Communications aux Sections 2, 4, 5 et 6: 113. 1954" under the title "Les sous-familles et les tribus des Rubiacées" I changed my attitude with regard to these genera, and accepted the decision taken by Baillon; a strong argument in favour of the view that they are to be included in the *Rubiaceae* is the presence of stipules provided with colleters, whereas a strong argument in favour of their exclusion from the *Loganiaceae* is to be found in the absence of intraxylary phloem; the presence of raphides and the valvate aestivation of the corolla lobes prove that they belong to the subfamily *Rubioideae*.

In my paper of 1934 I also excluded the genus *Perama* Aubl., wich indeed shows many unusual features, viz. rudimentary stipules, parallel-nerved leaves, the presence of but two calyx lobes, which on account of the position they occupy in the diagram were regarded by Baillon (Hist. d. Pl. **7**: 392. 1880) as bracteoles, the sometimes trimeric corolla, the trilocular ovary and the triquetrous seeds. The position of this genus was once more discussed by me in the introduction to my work on "The African Species of *Oldenlandia* L sensu Hiern et K. Schumann" (1952). In a note on p. 13 I pointed out that on account of the presence of raphides the genus is to be included in the subfamily *Rubioideae*, but that it can not be returned to the *Spermacoceae*, the tribe in which it had been put by Hooker as well as by Schumann, as it differs from the latter in the ascending ovules, the rudimentary stipules and the structure of the pollen grains, and that it is on account of its many unusual features to be referred to a tribe of its own, the *Perameae*.

III. THE SUBDIVISION OF THE RUBIACEAE

If we take into consideration that the family *Rubiaceae*, as was pointed out in the preceding chapter, still contains several genera of which it may rightly be doubted whether their inclusion in this family is justified, it will be no matter of surprise that the delimitation of the groups in which the family was divided in the older works in which a classification of the family was given, was still far from satisfactory, for if it really had been satisfactory, the fact that these genera were included in it and that, as will be shown in this chapter, an even much larger number was referred to the wrong tribe, would be inexplicable. My attempts to correct these mistakes of my predecessors has led to the development of a new classification, but before entering into details, it seems appropriate to give a brief survey of the older ones.

The oldest subdivision of the *Rubiaceae* which deserves our attention, is that given by DE JUSSIEU on p. 196 of his "Genera Plantarum" (1789). He distinguished ten groups, mainly on account of the dehiscence or indehiscence of the fruit, the number of locules it contains and the number of seeds in the latter, though the number of stamens, the position of the leaves and the habit are also taken into consideration; in one of the groups, the last one, special emphasis is laid on the form of the inflorescence; it comprises the genera with capitate flowers. Only a few of the groups distinguished by de Jussieu can be regarded as natural or more or less so. Group I (Fructus dicoccus dispermus. Stamina saepius quattuor. *Folia plerumque verticillata*; *caulis plerumque herbaceus*) comprises the genera which are now included in the *Rubieae* (*Stellatae*, *Galieae*) and, in addition, the genus *Anthospermum*. Group II (Fructus dicoccus dispermus. Stamina quattuor, rarius quinque aut sex. *Folia saepius opposita*, *mediante vagina ciliata*; *caulis plerumque herbaceus*) agrees in the main with the *Spermacoceae*, though the genus *Knoxia* and, by mistake, the genus *Houstonia* have also been included. Group III (Fructus monocarpus bilocularis polyspermus. Stamina quattuor. *Folia opposita*; *caulis herbaceus aut frutescens*) comprises genera which for the greater part are referred by me to the *Hedyotideae*. Group IV (Fructus monocarpus bilocularis polyspermus. Stamina quinque. *Folia opposita*; *caulis saepe frutescens*) forms a rather unnatural mixture, for it contains genera which at present are referred to the *Hedyotideae*, the *Gardenieae*, the *Mussaendeae*, the *Cinchoneae* and the *Rondeletieae*. Group V (Fructus monocarpus bilocularis dispermus. Stamina sex aut plura. *Folia opposita*; *caulis frutescens aut arboreus*) comprises but two genera, viz. *Hillia* and *Duroia*, of which *Hillia* occupies a very isolated position in the family, whereas *Duroia* agrees in all essential points with the *Gardenieae*. Group VI (Fructus monocarpus bilocularis dispermus. Stamina quattuor. *Folia opposita*; *caulis plerumque frutescens*) contains genera which at present are included in the *Ixoreae*, the *Coussareae* and the *Guettardeae*. Group VII (Fructus monocarpus bilocularis dispermus. Stamina quinque. *Folia opposita*; *caulis frutescens aut arboreus*) comprises a mixture of genera now included in the *Psychotrieae*, the *Paederieae*, the *Anthospermeae*, the *Ixoreae*, the *Chiocceae* and the *Vanguerieae* and two genera which do not answer the description viz. *Chimarrhis* and *Simira*. Group VIII (Fructus monocarpus multilocularis loculis monospermis. Stamina quattuor aut quinque aut plura. *Folia opposita; caulis saepe frutescens*) comprises genera which are now included in the *Guettardeae*, *Chiococceae*, *Ixoreae*, *Vanguerieae* and *Psychotrieae*. Group IX (Fructus monocarpus multilocularis loculis polyspermis. Stamina quinque aut plura. *Folia saepius opposita; frutices aut herbae*) contains but three genera, viz. *Hamelia* (*Hamelieae*) *Patima* and *Sabicea* (since then included in the *Mussaendeae*, from where *Sabicea* was removed by me to a tribe of its own; the position of *Patima* is still uncertain). Group X (Flores aggregati supra receptaculum commune aut rarius coadunati. *Folia opposita*; *arbores aut frutices*, *rarius herbae*) comprises a number of unrelated genera which are now divided over the *Anthospermeae*, *Gardenieae*, *Coussareae*, *Psychotrieae*, *Morindeae* and *Naucleeae* and one genus of which the position is still uncertain, viz. *Cephalanthus*. In a remark made on p. 210 he unites these groups in four more comprehensive ones, viz. one with didymous fruits which corresponds with the groups I, II and III, one with two-seeded fruits, corresponding with the groups VI and VII, one with many-seeded fruits, corresponding with the groups IV and V, and one with plurilocular fruits corresponding with the groups VIII and IX; for his group X there is apparently no place in this classification. De Jussieu's ten groups were accepted with a few additions and emendations by Jaume de Saint-Hilaire in his "Exposition des familles naturelles" (I. 2: 428–453. 1805), whereas de Candolle's original division of the *Rubiaceae* in four tribes, viz. the *Stellatae*, *Coffeaceae*, *Chinchonaceae* and *Guettardaceae* (Ann. du Mus. **9**: 217. 1827) was apparently in the main based on the division made by de Jussieu in the above quoted remark.

In his "Mémoire sur la famille des Rubiaceés" (Paris, 1830) A. Richard distinguished 11 tribes, of which the first seven are characterized by the presence of a single ovule in each of the ovary cells, whereas in the four other tribes each of the ovary cells contains several ovules. The tribes with uni-ovular ovary cells are the *Asperuleae* (= *Rubieae*), *Anthospermeae*, *Operculariaceae*, *Spermacoceae* (in this tribe the genus *Cephalanthus* was included), *Coffeaceae* (contains genera which are now distributed over the *Psychotrieae*, *Coussareae*, *Paederieae*, *Ixoreae* and *Vanguerieae*), *Guettardaceae* (contains the genera with a drupe containing a bi- or plurilocular pyrene or several pyrenes, i.e. apart from the *Guettardeae* such totally different genera as *Saldinia*, *Nonatelia*, *Retiniphyllum*. *Lasianthus* and *Morinda*) and the *Cordiereae* (said to be intermediate between the *Guettardaceae* and the *Gardeniaceae*; it comprises three rather widely different genera, viz. *Cordiera*, *Myrmecodia* and *Tricalysia*). The tribes with pluri-ovular ovary cells are the *Hamelieae* (agreeing in the main with de Jussieu's group IX), the *Isertieae* (a small tribe differing from the preceding one in the fruit, which is a drupe containing 4–5 pyrenes; it contains the genera *Isertia*, *Gonzalea* (= *Gonzalagunia*), *Metabolus* and *Anthocephalus*), the *Gardeniaceae* (said to possess a berry with two locules, each with several seeds; it is a mixture of genera belonging to the *Gardenieae* and the *Mussaendeae* and contains in addition several genera which belong to other tribes or of which the position is still uncertain), and the *Cinchoneae* (with bilocular capsules with several seeds in each locule; it comprises besides the *Cinchoneae* genera belonging to the *Rondeletieae*, the *Naucleeae* and the *Hedyotideae* and genera occupying an isolated position, like *Sickingia* and *Hillia*). Richard based his classification therefore in the main on the number of ovules found in each of the ovary cells and on the nature of the fruit, but the characters by which the various kinds of fruits are distinguished, are morphologically of little or no importance, and practically no attempt has been made to correlate these differences with characters observed in other parts of the plants. It is therefore not to be wondered that but few of the tribes distinguished by him can be accepted as natural ones or more or less natural ones. This applies to the tribes *Asperuleae*, *Anthospermeae*, *Spermacoceae* and perhaps to the *Opercularieae*.

In the classification elaborated by DE CANDOLLE in the "Prodromus" (**4**: 342–343. 1830) 13 tribes are distinguished, of which the first five agree with each other in the presence of several seeds in the loculi of the fruit, whereas the other eight tribes have but a single seed in each of the loculi. To the first group belong the *Cinchonaceae* (whith bilocular capsules and winged seeds) subdivided in *Naucleae* (with sessile fruits) and *Cinchoneae* (with pedicellate fruits), the *Gardeniaceae* (with bilocular or occasionally by abortion unilocular fleshy fruits and seeds without wings) subdivided in *Sarcocephaleae* (with sessile, capitate fruits) and *Gardenieae* (with pedunculate or sessile, but not capitate fruits), the *Hedyotideae* (with bilocular capsules and seeds without wings) subdivided in *Rondeletieae* (with triangular, free stipules) and the *Hedyoteae* (with stipules that are at the base united into a sheath and at the top split in several narrow processes), the *Isertieae* (with drupes containing 2–6 pyrenes) and the *Hamelieae* (with berries containing several locules). The second group comprises the *Cordiereae* (with baccate, plurilocular fruits), the *Guettardaceae* (with drupes containing 2–10 pyrenes and cylindrical seeds) subdivided in *Morindeae* (with capitate or connate fruits) and *Guettardeae* (with more or less distinctly pedicellate fruits), the *Paederieae* (with but slightly fleshy fruits of which the fleshy parts are soon lost, after which the two flattened pyrenes remain attached to the top of the bipartite axis; seeds with a fleshy endosperm), the *Coffeaceae* (fruits said to be bilocular berries with two semiglobose seeds, the latter with a longitudinal groove on the flat side; endosperm horny) subdivided in *Coffeae* (with distinctly pedicellate fruits) and *Cephaelideae* (with capitate fruits surrounded by bracts), the *Spermacoceae* (with more or less dry fruits containing 2 to 4 pyrenes, and with a bilamellar stigma) subdivided in *Cephalantheae* (with sessile flowers), *Euspermacoceae* (with pedicellate flowers and fruits splitting into 2–4 mericarps and *Putorieae* (with a more or less fleshy fruit which does not split), the *Anthospermeae* (with a more or less dry fruit which splits into two mericarps or, more rarely, fleshy and bilocular, and with long and hairy stigmata), the *Stellatae* (with a more or less dry fruit which splits into two mericarps or, more rarely, fleshy and bilocular, and with capitate stigmata) and the *Operculariaceae* (with unilocular one-seeded connate fruits which finally open at the top with two valves).

If we compare the classification of de Candolle with that of Richard, we see that two new tribes have been added, viz. the *Paederieae*, which is to be regarded as a natural one, and the *Hedyotideae*, which comprises two subtribes, the *Rondeletieae* and the *Hedyoteae*, and as these subtribes show but a very superficial resemblance, this tribe is obviously an entirely artificial one. Some of the other tribes too are subdivided, but in the case of the *Gardeniaceae*, the *Guettardaceae* and the *Coffeaceae* these subdivisions merely emphasize the unnaturalness of the tribes which are divided in this way.

In the classification of LINDLEY (The Vegetable Kingdom: 761 and 768. 1846) the name of the family is changed into *Cinchonaceae*. This has apparently been done because one of the tribes, viz. that of the *Stellatae*, has been excluded; this tribe was raised by Lindley to family rank. The tribe *Cordiereae* has been suppressed, and the name *Coffeaceae* has been replaced by *Psychotridae*, but otherwise there are no differences of any importance with the classification of de Candolle.

In BENTHAM and HOOKER's "Genera Plantarum" (II, 1. 1837) HOOKER too splits the family on account of the number of ovules per ovary cell, but instead of two main groups, he distinguished three of them. Series A comprises the tribes with pluri-ovular ovary cells, series B those with collateral ovules, and series C those with uni-ovular ovary cells. Series A and series C, moreover, are each subdivided in two subseries; series A according to the nature of the fruit in a subseries with dry fruits and one with fleshy fruits, and series C according to the position of the embryo in the seed in a subseries in which the radicle points downwards and one in which the radicle points upwards. In the first subseries of series A two of the subtribes created by de Candolle, viz. the *Naucleae* and the *Rondeletieae* are raised to the rank of tribes, whereas an entirely new tribe, that of the *Henriquezieae*, is added; however, the two genera brought together in this tribe show no distinct affinity with the *Rubiaceae*, and the tribe therefore was excluded by me, and placed in the rank of a family in the vicinity of the *Bignoniaceae* (see chapter II). In the second subseries de Candolle's *Isertieae* are suppressed, whereas two new tribes, the *Mussaendeae* and the *Catesbaeeae* are added. Series B comprises two tribes, the *Cruckshanksieae* and the *Retiniphylleae*, of which the first shows an unmistakable resemblance to the *Hedyotideae*, a tribe in which it was sunk by Schumann, whereas the second was created for the aberrant genus *Retiniphyllum*, which by Richard was regarded as a near ally of *Nonatelia*, whereas it was put by Schumann in the *Gardenieae*; both authors, however, were mistaken, for as *Retiniphyllum* has no raphides, it can be no near ally of *Nonatelia*, a genus belonging to the *Psychotrieae*, and as it does not show the pollination mechanism which is typical for the *Gardenieae*, it can not be included in the latter either. In the first subseries of series C the *Morindeae* are removed from the neighbourhood of the *Guettardeae*, with which in fact they show no near affinity, and transferred to the second subseries, whereas four new tribes are added, viz. the *Knoxieae*, the *Chiococceae*, the *Alberteae* and the *Vanguerieae*. In the second subseries de Candolle's *Coffeae* are split into three tribes, viz. the *Ixoreae*, the *Psychotrieae* and the *Coussareae*. In comparing Hooker's classification with that of de Candolle, it strikes us that great importance is attributed to the aestivation of the corolla lobes, a point which in the classification of de Candolle played no part, and which enabled Hooker to separate the *Ixoreae* from the *Psychotrieae* and the *Coussareae*, and that in the series with uni-ovular ovary cells attention is paid to the position of the embryo in the seed (radicle either superior or inferior), i.e. to the insertion of the ovules; in the case of the *Guettardeae*, moreover, the attention is drawn to the absence or poor development of the endosperm. The total number of tribes distinguished by Hooker is 25 against 13 by de Candolle.

The classification adopted by K. SCHUMANN in Engler & Prantl's "Natürliche Pflanzenfamilien" (IV, **4**: 16. 1891) is in the main founded on that of Hooker. Schumann too begins with a division based on the number of ovules, but in contrast with Hooker he accepts but two main groups, for which he introduces the names *Cinchonoideae* and *Coffeoideae*. The *Cinchonoideae* are divided in *Cinchoninae* (with dry fruits) and *Gardeninae* (with fleshy fruits), the *Coffeoideae* on account of the position of the radicle in *Guettardinae* (radicle superior) and *Psychotriinae* (radicle inferior). In the *Cinchoninae* he includes six tribes, viz. the *Condamineae*, *Oldenlandieae* (= *Hedyotideae*), the *Rondeletieae*, the *Cinchoneae*, the *Henriquezieae* and the *Naucleeae*, the same tribes, therefore, as Hooker included in his subseries 1 of series A. The *Gardeninae* are divided in two tribes, the *Mussaendeae* and the *Gardenieae*, corresponding with the tribes VII and X of subseries 2 of Hooker's series A; the two other tribes which Hooker recognized in this subseries, the *Hamelieae* and the *Catesbaeeae*, are included by Schumann in the *Gardenieae*, which is no improvement, for these tribes have very little in common with each other and with the true *Gardenieae*. Of the two tribes for which Hooker created his series B, the first, the *Cruckshanksieae*, are included by Schumann in his *Oldenlandieae*, with which they are doubtless nearly related, whereas the *Retiniphylleae* were included by him in his *Gardenieae*, which, as pointed out above, was a mistake. The *Guettardinae* correspond to Hooker's series C subseries 1, and comprise the same five tribes, the *Alberteae*, *Knoxieae*, *Vanguerieae*, *Guettardeae* and *Chiococceae*. The *Psychotriinae* similarly correspond to Hooker's series C subseries 2, and comprise the same eight tribes, viz. the *Ixoreae*, *Psychotrieae*, *Paederieae*, *Anthospermeae*, *Coussareae*, *Morindeae*, *Spermacoceae* and *Galieae*. The differences with the classification elaborated by Hooker are therefore but few, and the characters on which the classification rests, are in the main the same.

The classifications discussed above are all based in the first place on the number of ovules per ovary cell, whereas for the subdivision of the main groups much weight was attached to the nature of the fruits, which to this end were distinguished in dry and fleshy ones, a distinction which is morphologically unsound and therefore taxonomically of little or no value, and subsequently also to the position of the radicle, which is certainly of importance, but of which nevertheless the importance has been overrated, for the *Guettardeae* show but little affinity to the other tribes of the *Guettardinae*, and the *Ixoreae* show more affinity with the latter than with the other tribes of the *Psychotriinae*, the group in which they were included by the authors of these classifications. This means that the *Guettardinae* and the *Psychotriinae* are to be regarded as artificial groups.

More recently, and so far only tentatively, two new classifications were proposed, which deviate considerably from the older ones. The first of these two new classifications is that which I myself expounded at one of the meetings of the section for taxonomy of the 8th Botanical Congress held in Paris in 1954, but as of this classification only a very brief report was published (Rapports et Communications aux sections 2, 4, 5 et 6: 113–114), and as I have since then changed my views on some points, I will first discuss the other one, as of the latter a more detailed report has been published. This is the one proposed by VERDCOURT (Remarks on the classification of the Rubiaceae in Bull. du Jard. bot. de l'État, Bruxelles, **28**: 209–281. 1958). Verdcourt distinguishes three subfamilies l.c. 250–252), viz. *Rubioideae* (raphides present and seeds albuminous), *Cinchonoideae* (raphides absent and seeds albuminous; hairs never septate) and *Guettardoideae* (raphides absent, seeds exalbuminous or with traces only of albumen). The *Rubioideae* are subdivided into *Psychotrieae*, *Coussareae*, *Morindeae*, *Schradereae*, *Urophylleae*, *Craterispermeae*, *Knoxieae*, *Paederieae*, *Coccocypseleae*, *Argostemmateae*, *Ophiorrhizeae*, *Hamelieae*, *Cruckshanksieae*, *Hedyotideae*, *Anthospermeae*, *Spermacoceae* and *Rubieae*. This subfamily therefore includes the tribes which were divided by me over two subfamilies, viz. the *Rubioideae* and the *Urophylloideae*. The last-mentioned subfamily is included by him on the ground that the styloid crystals of calcium oxalate differ too little from the true raphides, a view with which but few specialists in this field will agree. In my opinion there is very little resemblance between the tribes included in this subfamily and those which were united by me in the subfamily *Rubioideae*. With the introduction of the new tribe *Craterispermeae* and with the restoration of the *Cruckshanksieae* I agree. The *Cinchonoideae* comprise in Vercourt's delimitation the tribes *Naucleeae*, *Cinchoneae*, *Rondeletieae* (in which the *Condamineae* are included), *Mussaendeae*, *Catesbaeeae*, *Gardenieae*, *Ixoreae* (divided in *Ixorinae*, *Cremasporinae* and *Heinseniinae*,) *Retiniphylleae*, *Alberteae*, *Vanguerieae* and *Chiococceae*. These tribes were for reasons which I will expound hereafter, divided by me over two subfamilies, the *Cinchonoideae* and the *Ixoroideae*, which in my opinion have but little in common. The reduction of the tribe *Cremasporeae* to a subtribe of the *Ixoreae* is hardly justifiable; the genus *Heinsenia* was not seen by me, but Verdcourt's remarks on this genus do not prove a near affinity with the *Ixoreae*. With regard to his reduction of the *Condamineae* to the *Rondeletieae* I feel rather sceptical, but I admit that both tribes are very imperfectly known and deserve a thorough revision. In his third subfamily, that of the *Guettardoideae*, he recognizes but one tribe, the *Guettardeae*. In this point there is full agreement between his classification and mine.

I will now give a summary of the remarks on the classification of the *Rubiaceae* made by me in various papers on genera or groups of genera belonging to this family, and expound the classification at which I have finally arrived. This, however, is still a provisional one, for there are still a considerable number of genera of which the position remains uncertain. As I am unable to continue my work in this field, I must leave the study of these genera to others.

In the above-mentioned paper read at the 8th Botanical Congress I distinguished six subfamilies, viz. the *Cinchonoideae*, the *Urophylloideae*, the *Ophiorrhizoideae*, the *Guettardoideae*, the *Ixoroideae* and the *Rubioideae*. Since then I have added a seventh subfamily, that of the *Gleasonioideae* (see my paper "On the position of *Platycarpum* Humb. et Bonpl., *Henriquezia* Spruce ex Bth. and *Gleasonia* Standl." in Acta Bot. Neerl. **6**: 351–377. 1957), and in the present publication I will add an eighth one, the *Hillioideae*. Here, moreover, one of the tribes included in the *Ophiorrhizoideae*, the *Ophiorrhizeae*, is transferred to the *Urophylloideae*, so that for the remaining tribe, the *Pomazoteae* a new subfamily name had to be coined, viz. *Pomazotoideae*.

The **Cinchonoideae** are in the delimitation proposed by me easily recognizable by the structure of the testa, which consists of cells with vary large pits, occasionally accompanied by the ordinary, very minute ones; the large pits, however, are always confined to the basal wall; in the very thick lateral walls they are totally lacking. A second important diagnostic character is to be found in the elongated form of the placenta. Other general characters, though not confined to this subfamily, are the always multiovular ovary cells and the absence of raphides. Genera which show another kind of placentation and whose testa cells show another kind of sculpture, and, of course, also those in which raphides are present, should be excluded. This applies e.g. to the genus which for a long time was known as *Sickingia* Willd., but of which the correct name is *Simira* Aubl. (see my paper on "The identity of *Simira tinctoria* Aubl. in Acta Bot. Neerl. **3**: 150–153. 1954), to the genus *Gleasonia* Standl., to the *Hedyotideae* and to several genera provided with raphides which were included in the other tribes; these genera do not show the typical structure of the testa cells found in the true *Cinchonoideae* nor the type of placentation which is characteristic for the latter.

The **Urophylloideae** are still imperfectly characterizable. Their most striking feature are the large, thick-walled testa cells which differ from those found in the *Cinchonoideae* by the absence of the peculiar large pits which are typical for that subfamily. Testa cells of the same kind as those of the *Urophylloideae*, however, are found also in the *Coccocypseleae* and the *Schradereae*, tribes which differ from those included in the *Urophylloideae* by the presence of raphides. That this kind of crystals would be present in *Urophyllum* Wall., as reported by Solereder, is a mistake; in this genus and its allies calcium oxalate is present in the form of styloids.

The third subfamily, that of the **Pomazotoideae,** is characterized by a testa consisting of cells of which the basal wall shows an unusual kind of dots, which seem to consist of bundles of very small pits. In this subfamily too the ovary cells are always pluri-ovular and raphides are always absent.

The fourth subfamily is that of the **Gleasonioideae**. It agrees with the next subfamily, that of the *Guettardoideae*, in the exalbuminous seeds, but differs from them, and indeed from all other subfamilies of the *Rubiaceae* in the large size of the cotyledons. Other points of difference with the *Guettardoideae* are the absence of crystals in the wall of the hairs, the pluri-ovular ovary cells and the capsular fruit. In the wall structure of the testa cells they show some resemblance to the *Hillioideae*, with which they agree also in the pluri-ovular ovary cells and in the capsular fruits, but from which they differ in the absence of raphides, in the loculicidally dehiscent capsule and in the absence of the tuft of hairs at the top of the seed.

The fifth subfamily, that of the **Guettardoideae** agrees, as stated above, with the preceding subfamily in the exalbuminous seeds, but it differs conspicuously from the latter in the smaller size of the cotyledons, the uni-ovular ovary cells and the drupaceous fruits. A character in which this subtribe differs from all the other ones, is the presence of crystals of calcium oxalate in the wall of the hairs with which the various parts are covered. These crystals are absent only in the genus *Machaonia*, which, however, on account of the entirely different fruits, is to be excluded. In this subfamily too raphides are always absent.

The sixth subfamily, that of the **Ixoroideae**, comprises all those tribes in which the upper part of the style acts as a receptaculum pollinis, which means that the hairs by which it is covered, collect already before the flower opens, the pollen from the anthers; when the flower opens, the pollen grains can be removed by visiting insects, which may transport them to flowers which have reached the stage in which the stigmata are ready to receive them. Other important characters, though not confined to this subfamily, are the simple interpetiolar stipules, the insertion of the stamens in the corolla throat and the absence of raphides. At one time I thought that the pollination mechanism which is characteristic for this subfamily, was found also in the *Naucleeae* in their former delimitation and in the genus *Cephalanthus*, but this view afterwards appeared to be erroneous.

The seventh subfamily is that of the **Rubioideae**, which are characterized by the presence of raphides, a feature which it shares with the next subfamily, that of the Hillioideae, and by the either valvate or, rarely, imbricate aestivation of the corolla lobes.

The eighth and, at least for the moment, last subfamily, the **Hillioideae**, agrees, as stated above, with the preceding one in the presence of raphides, but differs from the latter by the contorted aestivation of the corolla lobes and from all other *Rubiaceae* in the presence of a tuft of hairs at the top of the seed. In the structure of the testa cells it shows some resemblance with the *Gleasonioideae* or it least to those species of *Gleasonia* of which fully mature seeds were available.

Of these eight subfamilies the *Chinchonoideae*, *Gleasonioideae*, *Guettardoideae*, *Ixoroideae*, *Rubioideae* and *Hillioideae* are doubtless natural groups, but this can not yet be said with the same degree of certitude of the *Urophylloideae* and the *Pomazotoideae*, for although the tribes that are referred to them, can apparently not be accommodated in any of the other subfamilies, it is as yet not fully certain that the points in which they agree, are of sufficient importance to unite some of them in a more comprehensive group.

Now that a preliminary survey of the subfamilies has been given, we will turn our attention to the tribes for whose accommodation they were established.

In the Cinchonoideae I include seven tribes, the *Cinchoneae*, the *Naucleeae*, the *Condamineae*, the *Rondeletieae*, the *Sipaneae*, the *Mussaendeae* and the *Sabiceeae*. In my paper read at the 8th Botanical Congress I included in this subfamily also a tribe which I called the *Manettieae*, but this was an inaccuracy, for, as I had pointed out already in my work on "The African Species of *Oldenlandia*" (p. 14), the genus *Manettia* L is in the possession of raphides, and is therefore to be included in the *Rubioideae*.

The **Cinchoneae** were in the delimitation accepted by the older authors a rather artificial conglomerate of genera. A comparatively large number of them are to be excluded on account of the presence of raphides. These genera are (see "The African Species of *Oldenlandia*", p. 14) *Bouvardia* Salisb., *Heterophyllaea* Hook. f., *Hindsia* Bth., *Hymenopogon* Wall., *Manettia* L, *Danais* Commerc. ex Vent., *Coursiana* Homolle and *Hillia* Jacq.; they were included in this tribe either on account of their winged seeds, a character which is of little importance so long as it is not proved that the wings may be regarded everywhere as homologous structures, or else (*Hillia*) because of their adnate placentas. Other genera that are to be removed, are *Crossopteryx* Fenzl and *Coptosapelta* Korth.; as these genera show the pollination mechanism which is typical for the *Ixoroideae*, they will have to be included in that subfamily. *Coptosapelta* would, according to Solereder, be provided with raphides, but this is a mistake. The position of some other genera is still uncertain. On the other hand, most of the genera which so far have been included in the *Naucleeae*, will have to be removed to the *Cinchoneae*, as they differ from the other genera of this tribe in the capituliform inflorescence only. These genera are *Adina* Salisb., *Mitragyne* Korth., *Uncaria* Schreb., *Neonauclea* Merr. and probably also *Anthocephalus* A. Rich. and *Breonia* A. Rich. On account of the capituliform inflorescence they might perhaps be united in a subtribe.

The **Naucleeae** are restricted by me to the genus *Nauclea* L in the sense in which it was defined by Merrill, i.e. as congeneric with *Sarcocephalus* Afzel. In this delimitation they are characterized by the presence of connate ovaries, fleshy compound fruits and but slightly winged seeds. The testa has not yet been studied, so that it is not fully certain that the inclusion of this tribe in the Cinchonoideae is justified. The position of the genus *Cephalanthus* L remains as yet uncertain. As each of the ovary cells contains but a single, pendulous ovule, it is very doubtful whether this genus can be included in the *Cinchonoideae*. It has sometimes been referred to the *Spermacoceae*, but this is certainly a mistake, as the ovules are not attached to the middle of the dissepiment, but to its top. Before its position can be determined, this genus will have to be studied in more detail.

The **Condamineae** differ from the *Cinchoneae* in the horizontal, not vertical, position of the ovules and in the not or but slightly winged seeds. In these two characters they agree with the *Rondeletieae*, from which they differ in the valvate aestivation of the corolla lobes.

The **Rondeletieae** differ from the *Condamineae* in the aestivation of the corolla lobes, which in this tribe is either imbricate or contorted. However, as these two types of aestivation are, in contrast to imbricate and valvate, but rarely met with in nearly related genera, it is not impossible that further study will lead to a splitting up of this tribe. Of the genera which so far have been included in the *Rondeletieae*, some will have to be removed for other reasons. This applies to the genus *Deppea* Cham. et Schlecht., which according to Solereder is provided with raphides, *Sickingia* Willd., which as I have shown elsewhere, is identical with *Simira* Aubl., and which on account of the structure of the testa is removed by me to the *Urophylloideae*, *Gleasonia* Standl., which is the type of my subfamily *Gleasonioideae*, and *Sipanea* Aubl. and *Limnosipanea* Hook. f., which on account of their herbaceous growth, a very unusual feature in the *Cinchonoideae*, are transferred to a tribe *Sipaneae*.

The **Sipaneae** are a small tribe containing but three genera; on account of their herbaceous growth they occupy a somewhat isolated position in the subfamily. These genera are *Sipanea* Aubl., *Virecta* Vahl and *Limnosipanea* Hook. f.

The **Mussaendeae** too are in my delimitation but a small tribe. Apart from the genus *Mussaenda* L and its nearest allies, the genera *Aphaenandra* Miq. and *Asemanthia* Ridl. it comprises the genera *Isertia* Schreb. and *Cassupa* Humb. et Bonpl. and perhaps a few other ones which are less well known, but the great majority of the genera which by the earlier authors were included in this tribe, are to be transferred to other ones, often even to tribes belonging to other subfamilies; some of them do not even belong to the *Rubiaceae*. The characteristic features of the genera which are left by me in the *Mussaendeae*, are the bifid or bipartite stipules, the valvate aestivation of the corolla lobes and the insertion of the ovules on a discoid placenta. Of the genera which were included in this tribe by Schumann, *Schradera* Vahl, *Lucinaea* DC, *Mycetia* Reinw., *Myrioneuron* R. Br. and *Coccocypselum* [P. Br.] Sw. are on account of the presence of raphides to be removed to the *Rubioideae*, whereas *Acranthera* Arn. ex Meisn., *Coptophyllum* Korth.¹), *Pleiocarpidia* K. Sch. (*Aulacodiscus* Hook. f. non Ehrenb.), *Urophyllum*

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¹) The name *Coptophyllum* Korth. used by Miquel for two specuies belonging to the genus *Pomazota* Ridl. should be rejected. In my "Monograph of the genus *Pomazota* Ridley" (Journ. Arnold Arbor. **28**: 186–203.1947) I did this because *Coptophyllum* Korth. is a later homonym of *Coptophyllum* Gardner. I overlooked at that time that *Coptophyllum* Korth. is inserted in the list of nomina generica conservanda: in fact, it never occurred to me that the name of a genus of which but three species had been described, all of them, moreover, plants which had but rarely been mentioned in the literature, might have been entered in this list! For the same reason I did not go very deeply into the question of the generic identity of the species described by Korthals; I even included it provisorily in *Pomazota*, viz. with the remark that it was a "species non satis nota". As since then, however, some new combinations in the genus *Coptophyllum* Korth. have been proposed, it seems indicated to discuss this question somewhat more in detail.

The type specimen of the species on which *Coptophyllum* Korth. was founded, is no longer available, and was probably already lost at the time at which Miquel described a second species. The description of the type species is very incomplete, so incomplete that it will be difficult and probably even impossible to identify this species. In the description of the first of the two species which were included by Miquel in this genus, the generic name was provided with an interrogation mark. That Miquel was not certain that this species really belonged to the same genus as the plant described by Korthals, evidently means that he had to rely only on the description of the latter, which, as stated above, is very incomplete. If he had seen the type specimen, he would not have felt any doubt, for *Pomazota* is an easily recognizable genus. That Miquel omitted the interrogation mark when he described his second species, is probably to be explained by assuming that he compared it with his first species and found it to be congeneric with that one.

If I am right in assuming that Miquel had to rely only on the description given by Korthals, and it seems to me that this can hardly be doubted, then he must have been struck by the fact that the corolla was described by Korthals as naked inside, the stipules as obtuse and the fruit as indehiscent, characters that are not found in the two species described by himself, and, in fact, in none of the other species described in the genus *Pomazota*; it is true, however, that Korthals put an interrogation mark behind "indehiscens".

Now, is it permitted to assume that there can be no doubt with regard to the taxonomic identity of the genus described by Korthals? This question can certainly not be answered in the affirmative, and we will therefore have to admit that Miquel made a mistake in referring his two new species to this genus of doubtful identity.

It is possible, of course, that Korthals made a mistake in describing the inside of the corolla tube as naked and another one in describing the stipules as obtuse, but in order to prove this we would have to produce specimens which in all other respects would agree with the description given by Korthals, and such specimens have as yet not been found. We will have to concede therefore that *Coptophyllum* Korth. is an unidentifiable name, and that its inclusion in the list of nomina generica conservanda was not justified. For the two species described by Miquel the generic name *Pomazota* has to be accepted.

Wall., *Pauridiantha* Hook. f. and *Praravinia* Korth. have to be excluded because their testa cells do not show the structure which is typical for the subfamily to which the *Mussaendeae* belong; the position of the genera *Tammsia* Karst., *Pentagonia* Bth., *Hippotis* Ruiz et Pav. and *Sommera* Schlecht. is, as was pointed out in chapter II, as yet uncertain; of *Tammsia* it is even very dubious whether it can be left in the family.

The **Sabiceeae** are excluded by me from the *Mussaendeae* because of the simple stipules, the axillary inflorescences and the very narrow testa cells. This tribe contains but a single genus, viz. *Sabicea* Aubl.

In the Urophylloideae I include the *Urophylleae*, the *Pauridiantheae* and, provisionally, the *Simireae* and the *Ophiorrhizeae*. Whether Verdcourt's *Heinsiinae*, which were included by him in the *Mussaendeae*, may perhaps be shifted to this subfamily, in which case this subtribe would have to be raised to the rank of a tribe, remains to be seen. Following Schumann's example. I would include in this taxon besides the genus *Heinsia* DC the genus *Bertiera* Aubl. The testa cells of *Bertiera* (The African Species of *Oldenlandia*, Tab. VIIb) agree in structure with those of the *Urophylloideae* (op. cit. Tab. IV b–h and Tab. Vb).

The **Urophylleae** are characterized by their dioecism, the plurilocular ovary with in each ovary cell two fully distinct, subpeltate placentas which are attached near the axis and shift as the fruit is ripening to the central part of the dissepiment, and the more or less distinctly spreading stigmata. This tribe comprises the genera *Urophyllum* Wall., *Antherostele* Brem., *Didymopogon* Brem., *Maschalocorymbus* Brem., *Pravinaria* Brem., *Praravinia* Korth., *Raphidura* Brem., *Leucolophus* Brem., *Lepidostoma* Brem., *Crobylanthus* Brem., *Pleiocarpidia* K. Sch. and *Stichianthus* Val.

The **Pauridiantheae** have bisexual, heterostylous flowers, a usually bilocular, more rarely a quadri- or a quinquelocular ovary with in each of the cells a false dissepiment extending from the top for some distance downwards, axillary placentas which at the top are incised by the false dissepiment and show therefore an obcordate shape, and stigmata which are either cohering or free, but never spreading. To this tribe belong the genera *Pauridiantha* Hook. f., *Pampletantha* Brem., *Stelechantha* Brem., *Commitheca* Brem., *Poecilocalyx* Brem. and *Rhipidantha* Brem. and possibly also *Temnopteryx* Hook. f. and *Pentaloncha* Hook. f.

The **Simireae** comprise but a single genus, viz. *Simira* Aubl., better known under the name *Sickingia* Willd. (see my paper on "The identity of *Simira tinctoria* Aubl. in Acta Bot. Neerl. **3**: 130–133. 1954). This genus shows in the structure of its testa cells a striking resemblance with the genera belonging to the two preceding tribes, but in other respects it differs considerably from them. Its most striking characters are found in the way in which the ovules are inserted on the placenta and in the large seeds which in the upper half extend into a wing. On account of the horizontal position of the ovules *Sickingia* was originally referred to the *Rondeletieae*, but in reality the resemblance is rather superficial, for the number of the ovules is much smaller than in the *Rondeletieae* and they form but two rows. The form and the mode of insertion of the wing is quite different from that found in the seeds of any other member of the family. The genus doubtless occupies a very isolated position in the family, but in order to decide whether it has correctly been referred to the *Urophylloideae* or not, it will have to be studied in more detail.

The same applies to the three genera which by me were included in the **Ophiorrhizeae**, viz. *Ophiorrhiza* L, *Spiradiclis* Bl. and *Virectaria* Brem. On account of the thick-walled testa cells they are provisionally referred to this subfamily. In the structure of the testa cells they show a very striking similarity (The African Species of *Oldenlandia*: Tab. IV a, b and c), but in other respects they differ rather conspicuously. According to Verdcourt *Ophiorrhiza* would contain raphides, but it is not impossible that he mistook styloid crystals for raphides. Of *Spiradiclis*, however, he says "leaves contain optically active oblongs which separate into numerous needle-shaped crystals", so that we will have to assume that here indeed raphides are present. In that case this genus at least would have to be returned to the *Hedyotideae*.

The Pomazotoideae contain so far but a single tribe, the **Pomazoteae**, which is characterized by a testa consisting of thin-walled cells with a basal wall which is either minutely dotted or more or less coarsely tuberculate. It comprises the genera *Pomazota* Ridl. (The African Species of *Oldenlandia*: Tab. IV i), *Klossia* Ridl., *Siderobombyx* Brem., *Xanthophytum* Reinw. ex Bl. (op. cit. Tab. VI f), *Lerchea* L (op. cit. Tab. IV j) and perhaps also *Paedicalyx* Pierre ex Pitard, *Keenania* Hook. f., *Campanocalyx* Val., *Polysolenia* Hook. f. and *Leptomischus* Drake. Most of these genera are still very imperfectly known; some of them were originally included in the *Hedyotideae*, from which they had to be removed on account of the absence of raphides, whereas others had been referred to the *Mussaendeae*, from which, as stated above, they differ in the structure of the testa.

The Gleasonioideae contain so far but a single genus, though it is not excluded that the species which so far have been referred to the latter, will prove to belong to more than one genus. The testa of *Gleasonia macrocalyx* Ducke is provided with most peculiar wartlets each consisting of several cells, but the structure of the mature cellwall could as yet not be studied as the available seeds were too young. In the two species of which ripe seeds were available, viz. *G. duidana* Standl., the type species, and *G. uaupensis* Ducke, the testa does not show any wartlets, but the walls show a distinct network of cross-bars (see my paper "On the position of *Platycarpum* Humb. et Bonpl., *Henriquezia* Spruce ex Bth. and *Gleasonia* Standl. in Acta Bot. Neerl. **6**: 351–377. 1957, fig. 7). The pollen grains are in this genus larger than in any other genus of the *Rubiaceae* in which they could be measured, and they are, moreover, united in tetrads (op. cit. fig. 3). Pollen grains that are united in tetrads, however, are not confined to this genus; they are e.g. a general feature in the genus *Randia* (Houst.) L sensu Fagerlind.

The fifth subfamily, that of the Guettardoideae, also contains but one tribe, that of the **Guettardeae**, but this tribe comprises a larger number of genera than the two preceding subfamilies. Of the genera which were included in this tribe by Schumann, *Machaonia* can, as stated above, not be maintained in this subfamily, and whether *Timonius* Rumph. (= *Abbottia* F. v. Müll.) with its totally different ovaries and fruits has rightly been referred to the same tribe as *Guettarda* L, looks very dubious.

In the sixth subfamily, the Ixoroideae, a quite considerable number of tribes are to be included, viz. the *Coptosapelteae*, *Acranthereae*, *Cremasporeae*, *Gardenieae*, *Ixoreae*, *Chiococceae* and *Vanguerieae*.

The tribe of the **Coptosapelteae** comprises in my delimitation the genera *Coptosapelta* Korth. and *Crossopteryx* Fenzl. According to VERDCOURT (l.c.: 239), the latter would have testa cells of which the wall is "pitted as in *Cinchona*", but this is an error, for the pits are smaller than in the latter, and they are, moreover, not confined to the basal ball, but are found also in the lateral ones (see his plate XVI, fig. Q). In *Hymenodictyon* Wall. and *Corynanthe* Welw., which, according to Verdcourt, would have the same pollination mechanism as *Coptosapelta* and *Crossopteryx*, the upper part of the style is not distinctly swollen and lacks the short hairs which in the *Ixoroideae* enable this part to function as receptaculum pollinis. *Hymenodictyon* and *Corynanthe*, moreover, can not be regarded as near allies of *Coptosapelta* and *Crossopteryx*, for the aestivation of their corolla lobes is valvate, whereas it is in *Coptosapelta* and *Crossopteryx* contorted. Other characteristic features of *Coptosapelta* and *Crossopteryx* are the subglobose capsules, the pluriovular ovary cells and the short stipules.

The **Acranthereae** contain but a single genus, viz. *Acranthera* Arn. ex Meisn. (see my "Monograph of the genus *Acranthera* Arn. ex Meisn. in Journ. of the Arnold Arbor. **28**: 261–308. 1947). In this genus the receptaculum pollinis "remains included between the empty anthers and can be reached only through the windows between the projecting tips of the connectives" (l.c.: 273). On the same page I remarked "the connection of the stamens by means of the projecting tips of the connectives with the top of the style is a feature so entirely unparalleled in the *Rubiaceae* that one might feel inclined to regard the position of the genus with regard to the rest of the family as similar to that of the *Asclepiadaceae* with regard to the *Apocynaceae*, although in this way the importance of the connection between the anthers and the style is doubtless over-emphasized. It is perhaps more readily comparable to the way in which in the genera *Ceropegia* L and *Dichaelia* Harv. (*Asclepiadaceae*) the corolla-tips cohere." Other characteristic features of the species belonging to this genus are the herbaceous growth, the bilocular ovary with in each cell two elongated placentas inserted near the axis and attached over their whole length to the dissepiment, the reduplicate-valvate aestivation of the corolla lobes, the insertion of the stamens near the base of the corolla tube, the usually baccate, rarely more or less capsular fruits and the numerous small seeds provided with a fleshy endosperm and with a testa consisting of cells with a very densely punctate wall.

My next tribe is that of the **Cremasporeae**, which in the main agrees with the *Alberteae* of previous authors, but does not include the genera *Alberta* E. Mey, *Nematostylis* Hook. f. and *Belonophora* Hook. f. Verdcourt (l.c.: 248) also excludes *Heinsenia* K. Sch. and *Lamprothamnus* Hiern. *Heinsenia* may be allied to *Belonophora*, but the arguments on account of which *Lamprothamnus* was excluded by him, are not fully convincing. Before the exact position of these genera can be determined, they will have to be studied in more detail. The three first-mentioned genera were excluded by me because they do not show the pollination mechanism which is typical for the *Ixoroideae*. According to Verdcourt this would be an example of degeneration of the typical mechanism, but for this assumption no grounds are adduced. The typical *Cremasporeae* are characterized by the presence of a single pendulous ovule in each of the cells of the bilocular ovary and by the contorted aestivation of the corolla lobes.

The **Gardenieae** are in my delimitation a much smaller group than in that accepted by my predecessors. The delimitation given to this tribe by Hooker was widened by Schumann, who included in it the *Hamelieae*, a tribe of rather unnatural composition which nevertheless had been accepted by all his predecessors since the time of de Jussieu. The type of this taxon, the genus *Hamelia* Jacq., was removed by me, on account of the presence of raphides, to the subfamily *Rubioideae*. In the delimitation accepted by Hooker and in that accepted by Schumann the tribe of the *Gardenieae* comprises the genera *Tarenna* Gaertn. (= *Webera* Schrel. and *Chomelia* L.), *Enterospermum* Hiern., *Tricalysia* A. Rich., *Empogona* Hook. f. and *Morelia* A. Rich., which, on account of the structure of the drupe, were transferred by me to the *Ixoreae* (see p. 6–11 of my "Monograph of the genus *Pavetta* L" in Fedde's Repert. **37**: 1–208. 1934). Other genera that are to be excluded, are *Posoqueria* Aubl. and the related genus *Cladoceras* Brem. (in Hooker's Icones Plantarum t. 3411. 1940), which possess an entirely different pollination mechanism; the exact position of these two genera remains as yet uncertain. The true *Gardenieae* are easily recognizable by their many-seeded, comparatively large fruits which are provided with a thick, leathery or more or less woody pericarp and a gelatinous endocarp in which the numerous seeds are embedded. They are not rarely dioecious, in which case the male flowers are provided with a style of which the upper part serves as "receptaculum pollinis" (see my remarks on this group of genera in my "Monograph of the genus *Pavetta* L" p. 11–12). Fruits of the kind described above are found in the genera *Gardenia* Ellis, *Randia* Houst., *Rosenbergiodendron* Fagerl., *Tocoyena* Aubl., *Genipa* L, *Alibertia* A. Rich., *Ibetralia* Brem., *Duroia* L. f. and perhaps some other ones.

The **Ixoreae** are in my delimitation a larger group than in that of my predecessors, who restricted this tribe to genera with uni-ovular ovary cells. As the number of ovules per ovary cell appeared to vary in perfectly natural genera from one to two (*Pavetta* L) or from one to several (*Tarenna* Gaertn.), this restriction was dropped by me, and a comparatively large number of genera were, as stated above, transferred from the *Gardenieae* to this tribe. The two tribes resemble each other in the contorted aestivation of the corolla lobes. This is doubtless an important character, and for this reason the genera *Phyllomelia* Griseb. and *Strumpfia* Jacq., which show an imbricate aestivation of the corolla lobes, are to be excluded. Hooker said of these genera that they were "dubiae affinitatis", and today too the question of their taxonomic position has not yet been decided. Some other genera of doubtful position were discussed in my "Monograph of the genus *Pavetta* L", p. 8 and 9.

In the **Chiococceae** the ovary cells are always uni-ovular and the ovules always pendulous; another noteworthy feature is the insertion of the stamens near the base of the corolla tube. The only exception to this rule is found in the genus *Placocarpa* Hook. f. which for this reason will have to be excluded. The aestivation of the corolla lobes is either valvate or imbricate.

The last tribe to be included in this subfamily are the **Vanguerieae**. The genera belonging to this tribe resemble those belonging to the *Chiococceae* in the uni-ovular ovary cells and the pendulous ovules, which however are, as a rule, inserted below the top of the dissepiment; with the majority of these genera they agree furthermore in the valvate aestivation of the corolla lobes. One of the two most important points of difference between these two tribes is found in the insertion of the stamens; in the *Chiococceae* they are always inserted near the base of the corolla tube, in the *Vanguerieae* always in the corolla throat. The other important difference is found in the form of the "receptaculum pollinis", which in the *Vanguerieae* is short and swollen and at the base usually more or less free from the rest of the style, whereas it shows in the *Chiococceae* the same elongated, but slightly swollen form as in the other tribes of this subfamily. The genus *Craterispermum* Bth. lacks the swelling at the top of the style, and as it is provided with raphides and with heterostylous flowers it was removed by Verdcourt to the *Rubioideae*.

The Rubioideae are the largest subfamily of the *Rubiaceae*, and comprise in the survey given in this paper no less than nineteen tribes, and this number will probably increase when the genera of doubtful position become better known. They are, as we have seen, characterized by the presence of raphides and by the valvate or, rarely, imbricate aestivation of the corolla lobes. The only other subfamily in which the presence of raphides has been reported, is that created for the accommodation of the aberrant genus *Hillia* Jacq., where the corolla lobes show a contorted aestivation. The nineteen subfamilies of the *Rubioideae* are the *Hedyotideae*, *Cruckshanksieae*, *Argostemmatideae*, *Coccocypseleae*, *Schradereae*, *Hamelieae*, *Spermacoceae*, *Anthospermeae*, *Rubieae*, *Perameae*, *Psychotrieae*, *Triainolepideae*, *Lathraeocarpeae*, *Gaertnereae*, *Coussareae*, *Paederieae*, *Morindeae*, *Knoxieae* and *Craterispermeae.*

The **Hedyotideae** are by far the largest tribe of this subfamily. They comprise in my delimitation the genera which show a valvate aestivation of the corolla lobes, a character in which they agree with most of the other tribes, pluri-ovular ovary cells, a feature which returns in several other ones, a peltate placenta attached to the middle of the dissepiment, a mode of attachment which is found also in the *Hamelieae*, non-connivent anthers opening by slits, a point in which they differ from the *Argostemmatideae*, and a testa consisting of cells with a thin or at least not very thick wall. In my work on "The African Species of *Oldenlandia*" I transferred the genera *Bouvardia* Salisb., *Heterophyllaea* Hook. f., *Hindsia* Bth., *Manettia* Mutis ex L, *Danais* Commerc. ex Vent., *Coursiana* Homolle, *Hymenopogon* Wall., *Myrioneuron* R. Br. and *Mycetia* Reinw. from the *Cinchonoideae* to the *Hedyotideae.* The first seven genera had, on account of the winged seeds, been included in the *Cinchoneae*, whereas *Myrioneuron* and *Mycetia*, on account of their fleshy fruits, had been included in the *Mussaendeae*; all these genera, however, possess raphides and a testa consisting of cells which lack the large pits which are characteristic for the *Cinchonoideae. Myrioneuron* and *Mycetia* occupy a somewhat isolated position in the *Hedyotideae* on account of the fleshy fruits and on account of the simple, oblong stipules.

The genera that were excluded by me from the *Hedyotideae* comprise *Lerchea* L, *Pomazota* Ridl. and *Xanthophytum* Reinw. ex Bl., which were transferred to the *Pomazotoideae, Virectaria* Brem., *Spiradiclis* Bl. and *Ophiorrhiza* L, which were removed to the *Ophiorrhizeae*, a tribe which was provisionally included by me in the *Urophylloideae*, *Carlemannia* Bth. and *Sylvianthus* Hook. f., which, as pointed out in Chapter II, are to be excluded from the family, the genera *Carphalea* Juss., *Cruckshanksia* Hook. et Arn., *Dirichletia* Klotzsch, *Anotis* DC and *Jackia* Wall., which on account of the placenta arising from the basal part of the dissepiment and the small number of ovules are included in the *Cruckshanksieae*, and *Argostemma* Wall., *Clarkella* Hook. f. and perhaps *Neurocalyx* Hook. f., which on account of their connivent anthers and the insertion of the stamens on the basal part of the corolla tube are referred to a tribe *Argostemmatideae.* The position of the genus

Neurocalyx is not yet clear. If AIRY SHAW's section *Thyrsoideae* (Kew Bull. 1937: 281) really belongs to this genus, it will have to be transferred to the *Rondeletieae*, for in this section the walls of the testa cells show the structure which is typical for the *Cinchonoideae* (see "The African Species of *Oldenlandia*" Tab. II f).

The **Cruckshanksieae**, a tribe first recognized by Hooker, differ as stated above, from the *Heydyotideae* by the small number of ovules in the ovary cells (1 to 3 or 4) and the rod-like placentas rising from the base of the dissepiment. To this tribe belong the genera *Cruckshanksia* Hook. et Arn., *Carphalea* Juss., *Anotis* DC and probably the imperfectly known *Jackia* Wall. The genus *Dirichletia* Klotzsch is, according to Homolle (Bull. Soc. Bot. **93**: 613. 1936), identical with *Carphalea.*

The **Argostemmatideae** differ from the *Hedyotideae* in the connivent anthers opening with a short slit or a pore and in the insertion of the stamens at the base of the corolla tube. To this tribe belong the nearly related genera *Argostemma* Wall. and *Clarkella* Hook. f. and perhaps *Neurocalyx* Hook. f. (see the remarks made above on the position of the section *Thyrsoideae*).

The **Coccocypseleae** differ from the *Hedyotideae* in the simple stipules, the subcapitate flowers and the structure of the testa cells with their thick walls ("The African Species of *Oldenlandia*" Tab. III g), which are of the same type as those found in the *Schradereae* (op. cit. Tab. III h and i). To this tribe belong the genera *Coccocypselum* [P. Br.] Sw. and *Lipostoma* D. Don.

The **Schradereae** are the most deviating tribe among the *Rubioideae* with pluri-ovular ovary cells and valvate aestivation of the corolla lobes. The two genera included in this tribe, viz. *Schradera* Vahl and *Lucinaea* DC, were originally referred to the *Mussaendeae.* They are glabrous epiphytic shrublets with rather thick shoots, fleshy leaves and large deciduous stipules, usually climbing by means of adhesive rootlets; the inflorescences are capituliform; the flowers are provided with a cupular calyx; the fruits are baccate and the seeds are provided with a testa consisting of thick-walled cells which show a close resemblance to the testa cells of *Coccocypselum.*

The **Hamelieae** are in my delimitation restricted to the genera *Hamelia* Jacq. and *Hoffmannia* Sw., i.e. to those in which raphides are present. They resemble the preceding tribes in the pluri-ovular ovary cells, but differ from them in the imbricate aestivation of the corolla lobes. The difference between the valvate and the imbricate aestivation of the corolla lobes, however, is apparently of less importance than that between these two types of aestivation and the contorted one; in the *Psychotrieae* in which the aestivation is normally valvate, we meet at least two genera in which it is imbricate. For this reason the rather aberrant structure of the inflorescence found in the *Hamelieae*, a cyme with monochasial branches, is perhaps of more importance. The two genera, however, should be studied in more detail.

In the now following tribes the ovary cells contain but a single or, exceptionally (*Triainolepideae*), two or three collateral ovules and the aestivation is, with the exception of the genera *Naletonia* Brem. and *Notopleura* Brem. belonging to the *Psychotrieae*, where it is imbricate, always valvate.

The **Spermacoceae** are characterized by ovules which are attached to the middle of the dissepiment; in the seed the radicle points downwards, and in this respect there is agreement with the following tribes with the exception of the *Knoxieae* and the *Craterispermeae* where the radicle points upwards. The flowers are usually though not always 4-merous, and the fruits are either schizocarpous or capsular. The stipules are united in a truncate cylindrical sheath fringed with filiform appendages. The pollen grains are oblate and usually pluricolpate with short colpae. The genus *Perama* Aubl. was excluded because of its parallel-nerved leaves, rudimentary stipules, the two-lobed calyx, the pendulous ovules and the globose tricolporate pollen grains.

The **Anthospermeae** differ from the *Spermacoceae* in the position of the ovules, which are inserted on the basal part of the dissepiment; in this respect they resemble the following tribes with the exception of the *Knoxieae* and *Craterispermeae*. The style is usually split in two very long stigmata, and the stamens are usually inserted on the basal part of the corolla tube, but like the stigmata they project far beyond the mouth of the tube. The genera *Eleutheranthus* F. v. Müll., *Opercularia* Gaertn. and *Pomax* Soland., all three with unilocular ovaries, are apparently to be excluded, but before their position can be determined, they should be studied in more detail. The genus *Cremocarpon* Boiv. ex Boill. was transferred by me, on account of the horny endosperm, to the *Psychotrieae* (see my "Monographie des genres *Cremocarpon* Boiv. ex Baill. et *Pyragra* Brem." in Candollea **16**: 147–177. 1958). In the true *Anthospermeae* the endosperm is always fleshy.

The **Rubieae**, originally known as the *Stellatae* and afterwards as the *Galieae*, are characterized by the usually verticillate leaves, the rudimentary stipules, the usually rudimentary calyx, the didymous or by abortion occasionally globose fruits, the seeds adhering to the pericarp, the often strongly curved embryo and the globose pluricolpate pollen grains with their long colpae. That the stipules would not be rudimentary but on the contrary strongly developed and transformed into parts which are indistinguishable from true leaves, does not look very probable to me, as in the few *Galium* species which possess decussate leaves, distinct though small stipules are present, and as in the species with verticillate leaves never intermediate structures are met with. That at the nodes never more than two axillary shoots are formed, can not be regarded as a valuable argument for the stipular nature of the leaves which do not bear shoots in their axil, for in plants with verticillate leaves but rarely more than one or two of the axillary buds found at the same node develop into shoots. That the leaves may occur in whorls of 6 as well as of 8, and occasionally even of 7, is not favourable either for the view that part of them are stipules. Of the genera which so far have been included in this tribe *Didymaea* Hook. f. seems to be the only one of dubious position; it has well-developed stipules and seeds which do not adhere to the pericarp; it might perhaps be transferred to the *Anthospermeae*, but this deserves further study.

The **Perameae**, a tribe created for the accommodation of the genus *Perama* Aubl. which originally was included in the *Spermacoceae*, but which differs from the genera which are left by me in that tribe, by the parallel-nerved leaves, the rudimentary stipules, the insertion of the ovules at the base of the dissepiment and the two-lobed calyx. A two-lobed calyx is found also in *Declieuxia* H.B.K. and *Congdonia* Müll.-Arg., two genera which were referred to the *Psychotrieae*, but which occupy a rather isolated position in that tribe.

The **Psychotrieae** comprise a large number of genera, even though some of those which by previous authors were included in this tribe, had to be removed to other ones. This applies to the genus *Triainolepis* Hook. f., which on account of the collateral ovules and the plurilocular pyrene was made the type of a new tribe, the genera *Gaertnera* Lam. and *Pagamea* Aubl., which on account of the cylindrical stipular sheath and the almost completely superior ovary, were transferred to a tribe of their own, the *Gaertnereae*, and the genus *Thiersia* Baill. (= *Evea* Aubl.), which, as I could show ("Notes on the *Rubiaceae* of Surinam" in Rec. d. trav. bot. néerl. **31**: 278. 1934) is to be included in *Faramea* Aubl., i.e. in the tribe *Coussareae*. That the genera *Declieuxia* H.B.K. and *Congdonia* occupy a rather isolated position in the *Psychotrieae*, has already been pointed out. The most characteristic feature of the genera which are left by me in this tribe is the drupe with two or more pyrenes, which differ from those that are usually met with, in the thinness of the sclerenchymatous envelope. That in two of the genera, viz. in *Naletonia* Brem. and in *Notopleura* Brem., the valvate aestivation of the corolla lobes is substituted by an imbricate one, has already been mentioned.

The **Triainolepideae** differ from the *Psychotrieae* by their collateral ovules and by the presence of a single pyrene which, moreover, is provided with a thick sclerenchymatous envelope; another noteworthy feature are the stipules with their 3, 5 or 7 filiform lobes which are crowned by a colleter (see my "Monographie des Triainolepidées, tribu nouvelle des Rubioidées" in Proc. Kon. Ned. Akad. v. Wetensch. Ser. C, **59**: 1–21. 1956). The tribe comprises three genera, viz. *Triainolopis* Hook. f., *Paratriaina* Brem. and *Thyridocalyx* Brem.

The **Lathraeocarpeae** agree with the *Triainolepideae* in the structure of the fruit with its bony plurilocular pyrene, but they differ from them by the presence of but a single ovule in each of the ovary cells and by the pluricolporate instead of tricolporate pollen grains; the stipules, moreover, are united with the base of the sessile leaves and are produced into 1 or 2 stiff points. From the *Psychotrieae* and most of the other tribes of the *Rubioideae* they differ in the fleshy instead of horny endosperm (see my paper called "Les Lathraeocarpées, tribu nouvelle des Rubioidées" in Bull. Jard. Bot. de l'État Bruxelles **27**: 159–166. 1957). This tribe contains but a single genus, viz. *Lathraeocarpa* Brem.

The **Gaertnereae** are an often discussed group which on account of the almost entirely superior ovary seems to occupy a more or less anomalous position in the *Rubiaceae*, and which on account of this feature was referred by various authors, and at one time by me too, to the *Loganiaceae*. They are, however, provided with raphides, a form of crystals which is never met with in the true *Loganiaceae*, and lack the intraxylary phloem which is a characteristic feature of that family. Another point in which they differ from the *Loganiaceae* in the presence of colletors on the stipules. The almost entirely superior ovary, moreover, is not such an important feature as originally was assumed, because this condition is found also in some of the genera of the *Hedyotideae*. In most of their characters the *Gaertnereae* agree with the *Psychotrieae*; the most important difference, apart from the almost entirely superior ovary, is the union of the stipules into a long cylindrical sheath. The tribe contains but two genera, viz. *Gaertnera* Lam. and *Pagamea* Aubl.

The **Coussareae** come very near to the *Psychotrieae*, but are easily distinguishable from them by the nature of the dissepiment, which is very thin and which functions for a short time only, and by the presence of a single pyrene with a single seed. This tribe contains but two genera, viz. *Coussarca* Aubl. and *Faramea* Aubl.

The **Paederieae** differ from the *Psychotrieae* by the greater length of the stigmata and by the dry fruits. In its present delimitation this tribe makes a rather unnatural impression. The genus *Aitchisonia* Hemsl. is on account of the insertion of the stamens at various heights in the corolla tube and of the presence of glandular hairs certainly to be excluded; it may, as I have pointed out in the second chapter, belong to the *Dipsacales*, though the combination of glandular hairs and raphides has so far not been found in any of the families included in that order. The other genera doubtless belong to the *Rubiaceae*, but they differ so strongly from *Paederia* L that it seems hardly allowed to include them in the same tribe. They belong to the genera which should be studied in more detail.

The **Morindeae** agree with the *Spermacoceae* in the way in which the ovules are attached to the dissepiment, but they differ from them in habit and in the nature of the stipules, which though usually united in a sheath, are never provided with filiform appendages; in the genus *Didymoecium* Brem., probably a near ally of *Rennellia* Korth., *Tribrachya* Korth. and *Zeuxanthe* Ridl., the stipular sheath is produced into intrapetiolar lobes (see my paper on "Didymoecium genus novum Rubiacearum Morindearum" in Bull. Jard. Bot. de Buitenzorg, Ser. 3, **13**: 425–428. 1935, where a critical survey is given of the occurrence of intrapetiolar stipules in the *Rubiaceae*). The genera which were united in this tribe, are on the whole still imperfectly known.

The **Knoxieae** and the **Craterispermeae** differ from the other tribes of the *Rubioideae* with uni- or, rarely, biovular ovary cells in the position of the ovules; the latter are in these two tribes attached to the top of the dissepiment; in the seeds the radicle accordingly points upwards. The *Knoxieae* (*Knoxia* L and *Pentanisia* Harv.) are herbaceous plants, whereas the only genus of the *Craterispermeae* (*Craterispermum* Bth.) is shrubby. In the *Knoxieae* the stipules are usually fringed and in the *Craterispermeae* entire; the inflorescences, moreover, are in the *Knoxieae* terminal and in the *Craterispermeae* axillary.

The eighth subfamily, that of the *Hillioideae*, comprises but a single tribe, the **Hillieae**, and this tribe contains in my delimitation but a single genus, viz. *Hillia* Jacq. Noteworthy features of this genus are the presence of raphides, a character in which it agrees with the genera which are brought together in the *Rubioideae*, the contorted aestivation of the corolla lobes, a character in which it differs from all of them, and the presence of a tuft of hairs on the top of the seed, a character that is found nowhere else in the *Rubiaceae*. The wall of the testa cells shows a peculiar structure (see Tab. V a in my work on "The African Species of *Oldenlandia*"), which reminds one more or less of that found in the genus *Gleasonia* Standl., but in its other characters *Hillia* does not show any similarity whatever with this genus.

Among the genera showing a contorted aestivation of the corolla lobes there is one other genus which according to Solereder would contain raphides. This is the genus *Deppea* Cham. et Schlecht. However, as Solereder in some other instances too mistook styloid crystals for raphides, it is not impossible that this is an error. The genus, therefore, should be reinvestigated.

The survey given in the preceding pages of the results that since the appearance of the last general treatment of the *Rubiaceae*, viz. that of K. Schumann in Engler and Prantl's "Natürliche Pflanzenfamilien" (1891), have been obtained by the monographic treatment of a number of genera and tribes, will have left no doubt with regard to the insufficiency of the older classifications, but it will have shown at the same time that before a fully satisfactory classification can be obtained, a considerable number of genera will have to be reinvestigated. As I am myself unable to continue my work in this field, I must leave this to a younger generation.

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TARAXACUM LANJOUWII V. SOEST, A NEW SPECIES FROM SWITZERLAND

J. L. VAN SOEST
('s-Gravenhage)

(received November 29th, 1965)

Taraxacum lanjouwii v. Soest, spec. nov.
Planta ca. 10 cm alta, subaraneosa.

Folia numerosa sublutescentia, lobata, ad 12 cm longa petiolo pallido subalato inclusa; lobi laterales (utrinque 4–6) lingulati vel anguste triangulares, patentes, pro parte paulo retroversi vel suberecti, ad 17 mm longi, obtusi ad subacuti, saepe integrei vel dorso 1 dente vulgo grosso munito; interlobia ca. 5 mm lata, 5–10 mm longa, denticulata vel subdentata, angulis loborum subplicatulis; lobus terminalis subhastatus vel deltoideus, obtusus ad subobtusus, 10–15 mm longus, integer, lobulis basalibus triangularibus subobtusis.

Scapi floriferi foliis breviori ad subaequilongi, sub involucro araneosi.

Involucrum mediocre, 11–13 mm longum, 10–12 mm latum, subobscure olivaceo-viride. Squamae exteriores subadpressae, lanceolatae, pro parte lineares, ad 8 mm longae, immarginatae, interdum apice pro parte conspicue callosae; squamae interiores pro parte inconspicue callosae.

Galathium paulo radians, 2,5 cm diametro, saturate luteum. Ligulae marginales interdum ± canaliculatae, extus stria fusco-purpurea notatae; antherae polliniferae, stylus exsertus, stigmata fuscescentia.

Achenium fusco-stramineum, 3,5 mm longum (pyramide inclusa), superne spinulosum ceterum rugosum – basi laeve, in pyramidem brevissimam, 0,1 mm longam abrupte abiens. Rostrum subbreve (5–6 mm). Pappus albus, 5 mm longus.

TYPUS: Switzerland, Wallis, Saastal: Distelalp, 2150–2250 m, 17.7.1952, v. Soest (h. 31145, 31157); cotypus fructifer: Tälliboden, 2300–2400 m, 17.7.1952 v. S. (h. 31159).

Furthermore: Switzerland, Wallis, Zermatt, Schwarzsee, 2500–2600 m, VIII. 1965, v. Soest (h); Graubünden: Bernina pass, VII. 1948, v. S. (h); Parsennfurka above Bergün, 2300 m, 24.7.1954 v. S. (h).

This species belongs to sect. *Fontana* v. S., which, generally, can be found in subalpine regions from W. Switzerland eastward into the Balcans. It belongs to a subgroup, in which the flowers often are deep-yellow or nearly orange-coloured and in which the involucral bracts are often appressed, mostly dark-green and often pruinose. This subgroup is practically restricted to Wallis and Graubünden.

T. lanjouwii is nearly related to *T. aestivum* v. S.; the latter has less side lobes, a more pruinose involucre without gibbosities, badly developed pollen, less protruding styles and a more radiate flower head. The presence of gibbosities in *T. lanjouwii* is remarkable, though these are only poorly developed. There is no relation with the species of the section *Ceratophora* Dahlst., which has an arctic-alpine character and of which four species occur in the alpine region of Europe.

The subgroup may be described as follows.

Alpestria v. Soest:

Achemia rostrata, straminea, dilute brunnea vel ochracea ad pallide aurantiaca, saepe breviter spinulosa, interdum sublaevia; pyramide sat crassa, breviter conica; pappus albus.

Ligulae saturate luteae ad subaurantiacae. Involucra pruinosa; squamae leaves vel raro callosae, exteriores saepe adpressae.

Folia lingulata, lobata; lobi laterales saepe numerosae.

Subalpine and alpine regions from France to Austria: (1300–) 1800–2500 (–2800) m alt.

Type species: *T. reopliclum* v. S. 1959, published under sect. *Vulgaria Dahlst.*

Postcript

T. lanjouwii has recently been revised from a few other localities: Piemont, Gr. S. Bernardo, Alla Baux, 24.7.1899, Vaccari (FI); Val d'Aoste, Ceresola, Nivolet 2500–2600 m, 27.7.1910, Wilczek (FI); Wallis: Zermatt, Theodulweg gegen Lychenbretter 2620 m, 8.8.1922, Thellung (BAS); Lötschental, ob Ferden, 6.5.1938, W. Koch (ZT), kult. in ZT!; Hohe Tauern, Glocknergruppe, Finsteres Tal, Teischnitz 2600 m, 10.8.1953, Melzer (h).

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LA NOMENCLATURE AU SERVICE DE LA BOTANIQUE SYSTÉMATIQUE

W. ROBYNS

(Jardin Botanique de l'État, Bruxelles, Belgique)

(reçu le 30 octobre 1965)

La systématique scientifique, qui classe tous les êtres vivants, actuels et fossiles, d'après leurs affinités naturelles ou présumées telles, doit pouvoir donner à chaque taxon un nom stable, permettant de le désigner avec son rang taxonomique et de l'identifier facilement.

La nomenclature botanique n'échappe pas à cette exigence et depuis que C. Linné généralisa, en 1753, la nomenclature binominale, le besoin s'est fait sentir de compléter et de préciser, sur le plan international, les principes et les règles établis par l'illustre botaniste suédois.

Le premier essai dans ce sens eut lieu en 1867, au Congrès International de Botanique de Paris, qui adopta un premier recueil de "Lois de la Nomenclature Botanique" élaboré par Alphonse De Candolle.

Le IIe Congrès International de Botanique de Vienne 1905, revisa ce recueil, ce qui donna lieu, en 1906, à la publication par J. Briquet, rapporteur général, des "Règles internationales de la Nomenclature botanique", qui fixaient un point de départ de la nomenclature limitant le principe de priorité et prescrivaient une diagnose latine pour les groupes nouveaux. Une deuxième édition de ces Règles, mise au point par le même auteur, d'après les décisions du IIIe Congrès International de Botanique de Bruxelles 1910, parut en 1912.

Au Ve Congrès International de Botanique de Cambridge 1930, un compromis entre les botanistes de l'ancien et du nouveau monde rendit les Règles de Nomenclature internationales et universelles et y introduisit la méthode des types de nomenclature. Il donna lieu à une troisième édition des Règles qui, par suite du décès de J. Briquet, ne put malheureusement paraître qu'en 1935.

Au VIe Congrès International de Botanique, qui eut lieu à Amsterdam en 1935, T. A. Sprague était rapporteur général, mais, par suite des circonstances internationales, les décisions de ce Congrès ne donnèrent lieu, qu'en 1950, à la publication d'un supplément aux "Règles internationales de la Nomenclature botanique".

A partir du VIIe Congrès International de Botanique, tenu à Stockholm en 1950, la coopération internationale est devenue de plus en plus effective entre systématiciens du monde entier et la nomenclature en a largement profité. Sous la présidence du Professeur J. Lanjouw, un Comité de rédaction publia, en 1952, les décisions de ce Congrès, pour la première fois sous le titre de "Code International de la

Nomenclature Botanique". Il fut successivement revisé, amendé et réédité en 1956, après le VIIIe Congrès International de Botanique de Paris 1954 et en 1961, après le IXe Congrès International de Botanique de Montréal 1959. Les deux derniers Codes comprennent logiquement les divisions suivantes: I. Principes; Règles et Recommandations; III. Dispositions pour les amendements du Code.

Actuellement, un Comité de rédaction prépare, sous la présidence du Professeur Lanjouw, une nouvelle édition amendée du Code, d'après les décisions du Xe Congrès International de Botanique d'Edimbourg 1964.

Il va de soi qu'à la suite des revisions successives par les divers Congrès internationaux de botanique qui se sont succédés depuis 1867, le Code de Nomenclature est devenu de plus en plus extensif et de plus en plus détaillé et précis.

Alors qu'en 1912, les Règles comprenaient 58 articles avec XXXVIII Recommendations et I Appendice, le Code de Montréal 1961 comporte 75 articles avec 57 Recommandations, III Appendices, un guide pour la détermination des types et un guide pour la citation de la bibliographie botanique. Malgré cette extension, une uniformité de principes et une certaine stabilité des Règles ont pu être maintenues à travers les différentes éditions, mais surtout dans les deux derniers Codes, ou la séquence et la numérotation des Règles sont pratiquement restées identiques. Ceci est sans doute dû au fait qu'aux Congrès Internationaux de Paris 1954 et de Montréal 1959, les Sections de Nomenclature ont été plutôt conservatrices dans l'examen des modifications et additions proposées et que le Comité de rédaction a toujours oeuvré dans le même esprit.

Les botanistes disposent ainsi d'un instrument de travail précis et d'un guide irremplaçable, qu'ils doivent certes à A. de Candolle, J. Briquet et T. A. Sprague, mais surtout au Professeur Lanjouw qui, depuis le Congrès de Stockholm 1950, en sa double fonction de rapporteur général et de président du Comité de rédaction, a su maintenir au Code, à travers de multiples difficultés, son intégrité et son standing, rendant ainsi d'éminents services à la botanique systématique.

Pour être pratique et utile, un Code de Nomenclature doit être simple et assurer une continuité et une stabilité dans l'application des noms, depuis la date adoptée comme point de départ pour la priorité de la publication.

On reproche volontiers au Code actuel sa trop grande complexité, due à des réglementations entrant dans trop de détails et à l'existence de divers cas d'exception aux Règles. Une telle situation est cependant inévitable dans une codification universelle, s'appliquant à une science en plein développement et dont tous les acteurs ont la possibilité de proposer des amendements à chaque Congrès International de Botanique, soit à intervalles de 4 ou 5 ans, pratiquement réduits à 2 ou 3 ans par suite de la date de parution de chaque nouvelle édition du Code.

Conscients des inconvénients multiples de cette situation pour la stabilité et le bon renom du Code, le Comité de rédaction du Code de Montréal, au cours de sa session de Bruxelles, en novembre 1960, avait unanimement décidé de soumettre au prochain Congrés International de Botanique une proposition de procédure, visant à ne plus admettre de modifications et d'amendements au Code proprement dit, qu'à un Congrès international sur deux, sauf si l'intervalle entre deux Congrès est au moins de 8 ans[1]).

Cette période minimum était en effet jugée indispensable pour permettre aux systématiciens de se familiariser avec les données du Code en vigueur et d'en mesurer toutes les conséquences pratiques, afin de pouvoir proposer de nouveaux changements en parfaite connaissance de cause.

Malheureusement, au dernier Congrès d'Edimbourg 1964, cette sage proposition fut rejetée au vote par la Section de Nomenclature, alors qu'elle avait été adoptée par une large majorité au vote préliminaire par correspondance.

Cette décision est d'autant plus regrettable que certaines modifications introduites dans le Code n'ont pas été faites pour assurer la stabilité de la nomenclature ni pour suivre des usages établis de longue date. Parmi d'autres, nous ne prenons ici comme exemple que la Recommandation relative à la graphie des noms spécifiques dérivant de noms de personnes, représentant des noms vernaculaires ou d'anciens noms de genre. Alors qu'il était d'usage courant d'écrire ces noms avec une majuscule, la Section de Nomenclature du Congrès International de Stockholm 1950 a rendu cet usage facultatif, préférant ainsi une solution de facilité à la stabilité des noms. Elle devait entraîner une fâcheuse exception à l'article 73 (Code de 1961), prescrivant le maintien de la graphie originale d'un nom ou d'une épithète, sous prétexte que les majuscules ou les minuscules relèvent de la typographie et non de la graphie originale!

D'autres dangers, bien plus graves, guettent le Code lorsqu'il sort de son domaine pour s'immiscer dans celui de la systématique et prendre position dans des notions ou dans des concepts taxonomiques souvent controversés. C'est ainsi que le Comité de rédaction a eu à connaître des termes de diagnose et de description, afin d'en inclure une définition dans le Code. Il en fut de même du terme monstruosité.

De telles définitions ne nous paraissent pas à leur place dans un Code de Nomenclature, qui doit se contenter de définir les termes nomenclaturaux, afin d'en assurer l'emploi uniforme par tous les systématiciens.

On ne peut que regretter, à ce point de vue, que, depuis 1952, les Codes de Nomenclature aient cru devoir se préoccuper des notions de certains taxa. L'article 25 (Codes de 1956 et de 1961) adopte même une définition de l'espèce et des taxa inférieurs en "matière de nomenclature", qui produit automatiquement des taxa subordonnés comprenant le type nomenclatural du taxon immédiatement supérieur[2]). La même procédure s'applique à la sous-famille (art. 19), au sous-genre et à la section mais pas aux subdivisions de la section (art. 22), ainsi qu'aux taxa infraspécifiques (art. 26).

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[1]) Cfr A. C. Smith, The 1960 meeting of the editorial committee of the international code of Botanical Nomenclature. Taxon X, p. 12 (1961) et aussi Taxon XII, p. 111–112 (1963).

Les noms ainsi automatiquement créés constituent un groupe nouveau, à savoir les *taxa nomenclaturaux*, qui doivent être cités sans nom d'auteur, contrairement à l'article 46. Cette dérogation à la citation des noms d'auteurs "aux fins de précision" ne peut provoquer que de l'imprécision dans la botanique systématique.

En sortant de son domaine, le Code de Nomenclature a ainsi créé une situation pour le moins ambigue, dont il ne paraît possible de sortir qu'en laissant à chaque taxonomiste la liberté de s'exprimer conformément à ses concepts et à ses convictions.

Puissent les futurs Congrès Internationaux de Botanique y être toujours attentifs et conserver au Code son rôle propre et indispensable, au seul service de la systématique!

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[2]) Cfr. Ch. Baehni, L'interprétation de l'article 25 du Code de la nomenclature. Bull. Jard. Bot. État Brux., volume jubilaire Walter Robyns, XXVII, p. 167–172 (1957).

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THE SYSTEMATIC POSITION OF THE EAST MALESIAN GENUS HOLLRUNGIA K. SCH. WITHIN THE PASSIFLORACAE

C. G. G. J. VAN STEENIS
(Rijksherbarium, Leiden)

(received October 15th, 1965)

In 1888 K. Schumann described a new, monotypic genus of the *Passifloraceae* from Papua, *Hollrungia aurantioides* K. Sch. (Bot. Jahrb. **9**: 212). Its generic distinction was largely ascribed to the peculiar sessile, cap-shaped, undivided stigma ("tellerformige Narbe") and a 3-angular ovary.

Harms, who elaborated *Passifloraceae* for the first and second editions of the "Pflanzenfamilien", provided a figure of a section of the flower and a cross-section of the ovary (l.c. 3, 6a: 86, fig. 25 E–F. 1893, and 21: 495, fig. 218 E–F. 1925), maintaining Schumann's observation that *Hollrungia* possesses an androgynophore which brings it alongside *Passiflora*, but differing from that genus by the undivided cap-shaped stigma. This kind of stigma is rare in the *Passifloraceae* and Harms recorded it in the family only for two other, monotypic African genera *Crossostemma* and *Schlechterina*.

For a long time *Hollrungia* was known only from the type collection (Hollrung 62) which was unfortunately destroyed at Berlin during the second world war. However, many new collections were made since then, although sometimes referred to *Adenia* or *Passiflora* by sight identification, and the spotting of *Hollrungia* in the Moluccas induced me to publish some records (Reinwardtia 1: 480. 1952) and suggest a closer affinity with *Adenia*, not *Passiflora*.

Recently Dr. J. Hutchinson suggested to me to examine the genus more closely and this was made easy by excellent material from the Solomon Is. collected by Dr. Whitmore n. BSIP 4071, with both flowers and bud. This was supplemented by a fruiting specimen Brass 3283 found under *Adenia* sp.

This examination led to the fairly surprising result that *Hollrungia* has only seemingly an androgynophore: the staminal tube formed by the halfway connate filaments closely envelops the gynophore but is not at all adnate. Furthermore, it has appeared that only in the bud stage and young flowers the stigma appears as a fleshy, more or less solid cap, but that in later stages it expands into 3 short, distinct lobed stigmas, faintly reminiscing to the unfolding of a cauliflower. Schumann had obviously only buds and very young flowers at his disposal which served for Harms's drawings. Obviously the flowers of *Hollrungia* are protandrous, because in these young flowers the anthers are sometimes already opened. Protandry is also known to occur in *Passiflora*. Fig. 1–5.

In another new collection, Brass 27422 from Misima I., east of New Guinea, essentially the same structure was encountered, but here the ripe stigmas are not what Harms called "foliaceous" stigmas, those just mentioned, but are brush-shaped or cristate similarly as Harms figured for *Adenia obtusa* (cf. l.c. 21: 489, fig. 223B). Fig. 6. Also here the stigma appears in bud as an almost solid cap, but unfolds later. Fig. 7.

It seems to me that two different species are concerned. The great trouble appears now that we are in the dark about the question how the mature stigma would be in the type species, *H. aurantioides* K. Sch.

Anyway, it appears clearly that *Hollrungia* has the closest affinity with *Adenia* and not with *Passiflora*, although in the herbarium preliminarily identified specimens are found under all three generic names.

Then I paid attention to occurrence of tendrils. As I noted (l.c.) the Moluccan specimen Beguin 1535 has small tendrils *in* the inflorescences, that is, in the bifurcation of the cymose inflorescence, replacing so to say the central flower in the first, main dichasial fork, similarly as is found in several other genera of the family, e.g. *Adenia*, *Triphostemma*, etc. Such tiny tendrils one can also find sometimes in *Passiflora*, e.g. in the Malesian species *P. horsfieldii* and *P. moluccana* where they occur between the two main branches of the inflorescence and a common peduncle is virtually absent. Killip, in his monograph of the American species, also noted the occasional occurrence of such tendrils: "in a few species tendrils terminate peduncles and in one species some of the tendrils are axillary and some develop from a flowerless fork of a bifurcate peduncle".

Besides the inflorescential tendrils, both in *Adenia* and in *Passiflora* axillary tendrils occur and they are often accrescent and develop into strong, woody tendrils. If I am right in assuming that Brass 12880, an older, fruiting specimen from New Guinea, is a *Hollrungia*, than also this genus would share this character. As is well-known in climbing plants with tendrils, the latter are often very unfrequently collected and do not appear to be present in all sheets. Many collectors do not pay sufficient attention to such organs in lianas where they appear often lower down, and escape attention when only flowering tips are harvested. I find it for this reason premature to use the absence or presence of axillary tendrils to discriminate between *Hollrungia* on the one hand and *Adenia* and *Passiflora* on the other.

Also in the fruit *Hollrungia* cannot well be distinguished from the other genera; its fruit is indehiscent, but this can occur also in *Passiflora* and *Adenia* pro parte.

The seeds of *Hollrungia* are trabeculate and winged (by the dried aril?); whether here a distinctive character can be found must be decided by more ample field observation and a closer study in the other two genera.

A vegetative character which seems worthy of notice is the fact that *Hollrungia* has glands on the petiole, as in *Passiflora*, whereas in the *Adenias* known to me from Malesia, the leaves possess always two, almost saccate, auriculiform lobes at the base of the blade. But *Adenia* is a very large genus outside Malesia and I felt it beyond the scope of the present survey to check this for all species.

A similar remark I have to make about the sexuality of the flowers: in *Hollrungia* the flowers are bisexual, but in Malesian *Adenia* they appear to be (always?) unisexual.

In order to synthesize my observations I have arranged the characters in the following key to the three genera:

Key to the genera

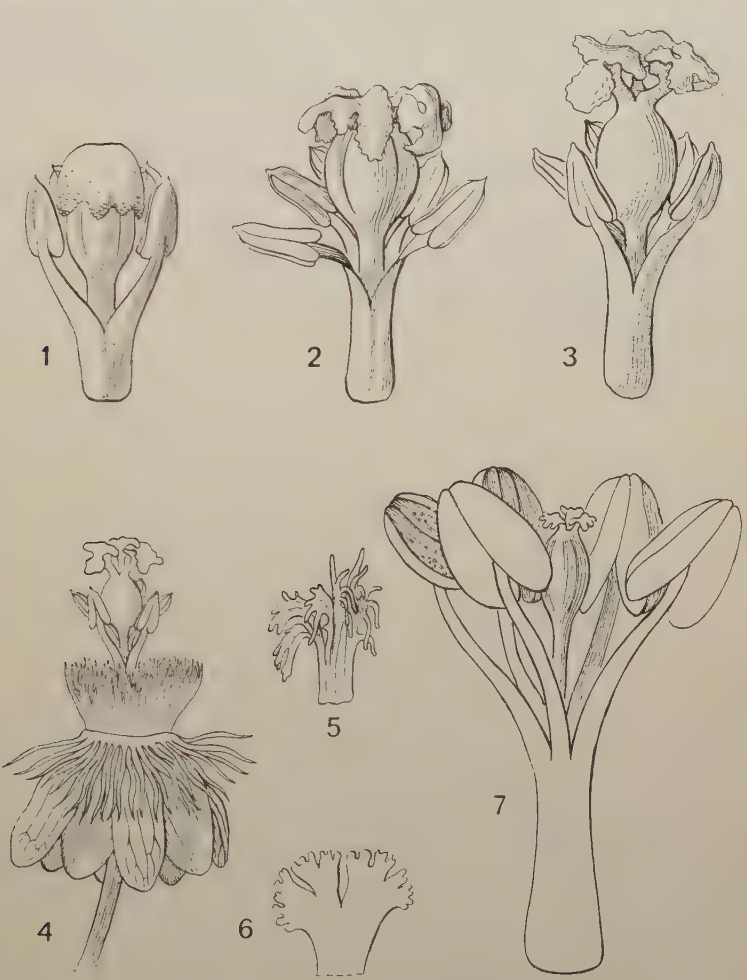
1. Androgynophore. Corona, a complicated structure. Flowers bisexual. Styles distinct; stigmas globular or club-shaped. Glands on petiole. Leaves with basal nerves . . . . **Passiflora**
1. Gynophore. Stamens in staminal tube. Styles distinct or indistinct, but stigmas not club-shaped or globular.
    2. Flowers bisexual. Leaf not with (subtri- or quintuplinervous) basal nerves. Two nectaries on margin of petiole. Inflorescence or tendril axillary or supra-axillary; also a serial bud. Small tendrils sometimes in inflorescence. Corona double, a complicated body of appendages and fringes. Filaments ribbon-like, halfway connate in tube, attached dorsally at incision of sagittate-oblong, blunt anthers. Styles 3, distinct, though thick and short, each bearing a lobed, flabby stigma or 3 more or less brush-like branched, short sessile stigmas (in bud stigma seemingly a cap-shaped solid body). Moluccas; New Guinea; Misima; Solomons . . . . **Hollrungia**
    2. Flowers (mostly? always?) unisexual. Leaf typically with basal nerves. Nectaries paired at underside of leaf-base, often saccate and auricle-like. Tendrils axillary; small ones in inflorescence. Inflorescence axillary. Corona single, simple, consisting mostly of 5 scales, rarely fringed. ♀ Styles and stigma as in *Hollrungia*, not as in *Passiflora*. ♂ Stamens said to be basifixed, not deeply sagittate, often narrow and apiculate . . . . **Adenia**

As to the specific discrimination I believe it premature to describe new species and I have accordingly marked the provisional taxa with the letters A, B and C. The material is distinctly heterogeneous, but this is in part due to the stage of collecting; fruiting specimens have thicker and larger leaves and more prominent nervation than those of flowering tips. Besides, lianas are often tricky plants as to leaf-shape which is very obvious in *Adenia* and has led to many superfluous names in that genus . Long ago I collected in the Anambas Is. a complete plant of an *Adenia* of which the lowest leaves were butterfly-shaped and the upper ones ovate-elliptic with all transitions between; this is preserved as a whole in the Bogor Herbarium.

I have the impression that the taxon indicated by the letter A is the same as the type, *H. aurantioides* K. Sch., of which the type specimen is lost. I base this suggestion on the fact that leaves and flowers are about of the same size and shape as those given in the type description;

only the pedicels are longer, but those of the type were taken from buds which may account for their shortness! Abundant topo-type material might lead to a considered decision. Probably taxon C is a distinct species, but whether this holds for B is uncertain as no open, mature flowers in various stages are known.

In order to enable herbarium curators to unearth the *Hollrungia* material which, as said before, is partly filed under incertae sedis of *Passiflora* and *Adenia*, the provisional key to the species is followed by an alphabetical-numerical enumeration of specimens known to me.



Figs. 1–5. Hollrungia sp. C. (Whitmore BSIP 4071)
1. Ovary and stamens from bud, × 5; 2. ditto, from just opened flowers, × 5; 3. ditto, in full anthesis, × 5; 4. ditto, flower, × 2½; 5. segment of inner corona, lateral view, × 5.

Figs. 6–7. Hollrungia sp. A (Brass 27422)
6. Unfolded stigma, × 10; 7. Sexual organs from semi-mature flower, × 5.

Provisional key to taxa of *Hollrungia*

A. Leaves elliptic, blunt. Inflorescences axillary. Flowers c. 8–10 mm long. Mature stigma in anthesis consisting of 3 obconical brushes without 'naked' styles. New Guinea; Misima I. Fig. 6–7.

B. Leaves ovate-oblong to oblong-elliptic, acute to acuminate, with mucronate tip. Flowers obviously smaller, but no mature flowers available. Inflorescences slightly to distinctly supra-axillary. Moluccas (Ternate I.); New Guinea.

C. Leaves oval, rounded, 10–12 by 5–7 cm, apex suddenly short-mucronate. Inflorescences from nearly axillary to distinctly supra-axillary. Flowers probably of same size as in B. Mature gynoecium with 3 distinct styles each with a flabellate (leafy) lobed stigma. Solomon Is. Fig. 1–5.

Enumeration of specimens of *Hollrungia*

Beguin 1535: B.
Brass 3283: C, published as *Passiflora moluccana* in J. Arn. Arb. 30: 44. 1949; 5239: not seen; 12880: B; 27387: A; 27422: A; 27551: A.
Carr 12905: B; 14876: B.
Clemens 2153: A; 5435: not seen.
Hollrung 62: not seen, type of *H. aurantioides* K.Sch.
Schram BW 6106: A.
Whitmore BSIP 4071: C.

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NOVITATES BURSERACEARUM III

J. J. SWART
(Botanical Museum and Herbarium, Utrecht)

(received September 22nd, 1965)

Protium aracouchini (Aubl.) March. var. **angustifolium** Swart n. var. Folia 1- usque ad 5-juga; interjugum basale petiolo plerumque longius sed interjugis aliis brevius; petioluli breves; foliola oblongo-lanceolata 7.5–10 cm longa, 2–2.75 cm lata, apicem versus distincte angustata, apice gradatim in acumen lineare sexies usque ad nonies longius quam latius acuminato; nervi sec. utrinque usque ad 20.

Holotypus: Lindeman 4504 (U, 078268B).

Surinam, south of Paramaribo, near Lelydorp, Lindeman 4504 (Aug. 1953) (U); between Suriname-river and Mapanecreek, Lindeman 4808 (Oct. 1953) (U); idem, Lindeman 4925 (Oct. 1953) (U).
British Guiana, Bartica-Potaro road, For. Dept. Br. Guiana 5608 (Mar. 1948) (K, U).

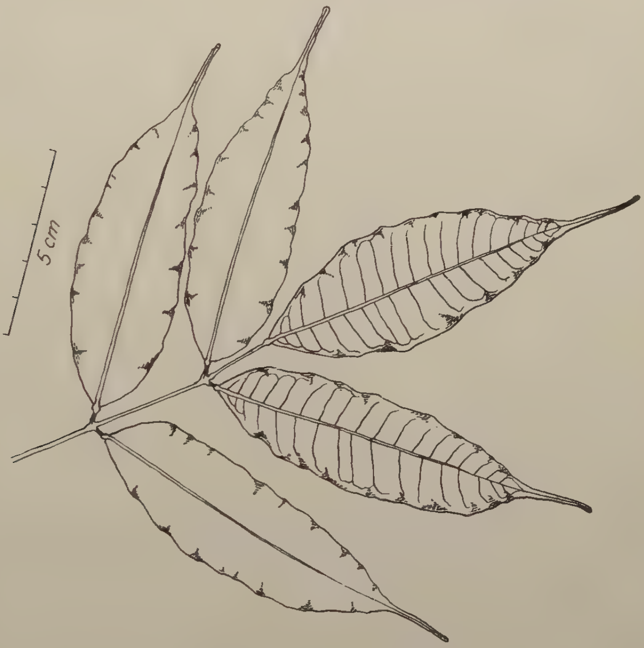

Fig. 1. *Protium aracouchini* (Aubl.) March. var. *angustifolium* Swart—Lindeman 4504 (U).

Protium copal (Schlecht. et Cham.) Engl. var. **matudea** Swart n. var. Folia magna usque ad 50 cm longa, 4-juga; foliolis terminalibus oblongis, non obovatis. Rhachis ramulisque inflorescentiae cum calyce et fructibus glabrescentes.

Holotypus: Matuda 3414 (K).

Mexico, Retiro, Tenosique, Matuda 3414 (Jun. 1939) (K); Rivina, Palenque, Matuda 3698 (Jul. 1939) (K).

Protium demerarense Swart n. sp. Arbor magna, usque as 24 m alta, 30–40 cm diam. Ramuli gracilioris angulosi glabri cinerei vel fusci lenticellis parvis brunneis obtectis. Folia 3-juga raro 1- aut 2-juga 20–30 (15–33) cm longa, petiolis semiteretibus basi subincrassatis 3.5–4.5 cm longis cum interjugis petiolulisque brevissime densiuscule pilosis, interjugis teretibus carinatis utrinque subincrassatis 3.5–4.5 cm longis, petiolulis semiteretibus vadoso-sulcatis utrinque incrassatis 0.75 (0.5–1.5) cm longis sed foliolorum terminalium teretibus carinatis 2.5–3 (2–4) cm longis, foliolis oblongis 9–14 cm longis 3–4.5 cm latis terminalibus prope basim angustatis lateralibus interdum apicem versus paulo angustatis, apice abruptius acuminatis acumine sublineari obtuso quinquies longiore quam latiore 10–15 mm longo 2–3 mm lato, basi cuneato, margine integro sed in sementibus prope apicem serratis, subcoriaceis glabris supra nitidis infra opacis, nervis lateralibus utrinque circ. 12 nervis, prim. facie superiore brevissime densiuscule pilosis, nervis ceteris totis glabris. Inflorescentiae axillares thyrsoideae e basi multiramosae fere glomeruliformes, usque ad 2.75 longae. Rhaches teretes striatae robustae cum bracteis bractolisque 0.5 mm longis pedicelisque sparse puberulae. Pedicelli teretes striati flori subaequilongi. Flores 5-meri 4 mm longi. Calyx cupuliformis circ. 1 mm altus glaber aut pilis nonnullis sparsis vestitus lobis semiorbicularibus subacuminatis tubo aequilongis. Petala subinduplicativo - valvata oblongo-lanceolata triangularia acuta apiculo incrassato inflexo. Stamina 10 in fl. masc. 2 mm longa filamenta subulata antheris oblongis triplo longiora. Discus annularis 10-lobus glaber circ. 0.25 mm altus. Pistillum in fl. masc. basi disco cinctum 0.75 mm altum ex ovario applanato-globoso 5-lobo 5-loculari pilis nonnullis adpressis sparso et stigmate sessili vel subsessili 5-lobo compositum. Drupa obliquo-oblonga utrinque subacuta 3.5 cm longa 1.5 cm diam. semper monoloculari monopyrena epicarpio lenticellis ellipticis numerosis obtecto mesocarpio tenui carnoso endocarpio tenui lignoso fragili.

Holotypus: For. Dept. Br. Guinea 3479 (U, 33160B).

British Guiana, Mahdia Creek, Potaro-river, at ± 100 m, Bartica-Potaro road, For. Dep. Br. Guiana 3479 (Jun. 1942, fl. masc.) (K, U); idem, For. Dep. Br. Guiana 3767 (Jan. 1943, fr.) (K, U); idem, For. Dep. Br. Guiana 3796 (Jan. 1943, fr.) (K); idem, For. Dep. Br. Guiana 4217 (1943, seedlings) (K, U).

Nom. vern.: "purokai".

This species resembles *Protium altsonii* Sandw. and *P. hostmannii* (Miq.) Engl., but the former species differs by its 4- to 7-jugate leaves bearing lanceolate to lanceolate-oblong leaflets with 14 to 17 pairs of sec. nerves, its smaller flowers with densely pilose ovary and its much smaller drupes. The latter differs by its usually 2-jugate

much shorter leaves, composed of a petiole shorter than the interjuga and of shorter, more elliptic leaflets with 10 pairs of sec. nerves and an acumen only 2- to 3-times as long as wide, by its 4-merous, much smaller flowers with a rather densely pilose ovary and by half-sized fruits.

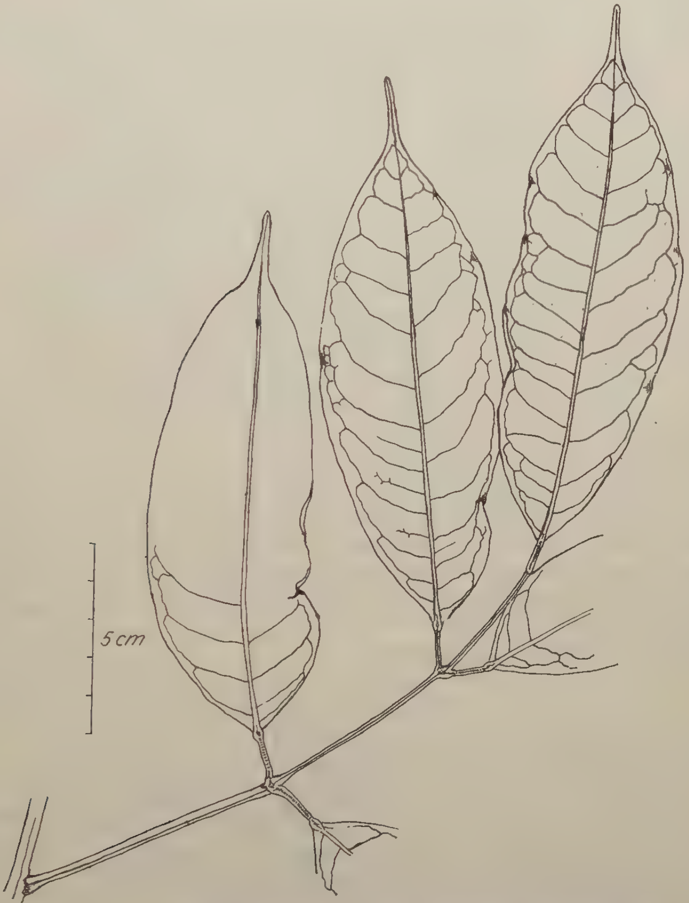

Fig. 2. *Protium demerarense* Swart — For. Dept. Br. Guiana 3479 (U).

Protium divaricatum Eng. var. **trijugum** Swart n. var. Folia 3-juga 25–30 cm longa, petiolis 4–7 cm longis, interjugis terete-carinatis 2–5 cm longis, nervis sec. foliolorum utrinque 10–11. Inflorescentiae interdum folio suffulcienti fere aequilongae minime 2/3 partes eorum aequantes. Rhachis ramuli et pedicellorum partes inferiores sparse puberuli.

Holotypus: Black 47–1507 (IAN).

Brazil, Amazonia, near Tefé, Black 47-1507 (Sep. 1947. fl. masc.) (IAN); id., id., Black 47-1529 (Sep. 1947, fl. masc.) (IAN).

Protium dusenii Swart n. sp. Arbor. Ramuli graciles teretes

striati glabri fusci. Folia 2- vel 3-juga 17 (14–23) cm longa ubique glabra, petiolis semiteretibus basi subincrassatis 3 cm longis, interjugis carinatis 2.5–3.5 cm longis, petiolulis foliolorum lateralium semiteretibus supra sulcatis 0.8 cm longis terminalibus teretibus 2 cm longis, foliolis oblongis 8.5 (6.5–11) cm longis 3 (2.5–4) cm latis basalibus brevioribus, foliolis prope basim acute cuneatam angustatis interdum etiam supra medium angustatis terminalibus a medio basim versus distincte angustatis, apice gradatim acuminatis acumine attenuato obtuso 6 mm longo 2 vel 3 mm lato, margine integro, subcoriaceis leavibus supra nitidis infra opacis, nervis sec. utrinque 10–12 nervis prim. prominentibus nervis sec. prominulis nervis tert. conspicuis. Inflorescentiae axillares glomeruliformes dense ramosae pauciflorae 1 cm diam. Rhaches teretes cum pedicellis teretibus 2–3 mm longis bracteis bracteolisque triangularibus obtusis 0.5 mm longis calycibus corollibusque superficie exteriore sparse puberulae. Flores 5-meri circ. 3 mm longi. Calyx cupuliformis 1 mm altus lobis triangularibus acutis tubo aequilongis. Petala elliptica apiculo acuto inflexo. Stamina 10 2 mm longa filamentis subulatis antheris oblongis. Discus annularis 10-lobus glaber. Pistillum 2 mm altum ex ovario ovoideo 5-sulcato sparse puberulo et stigmate sessili 5-lobo compositum.

Holotypus: Dusén 15296 (K).

Brazil, Parana, Serra da Prata, Dusén 15296 (Jul. 1914, fl. fem.) (K).

Protium dusenii Swart resembles *P. widgrenii* Engl., from which it differs by the indumentum of its flowers, specially of the ovary, the glomeruliform inflorescences and the less distinct narrowing of the leaflets.

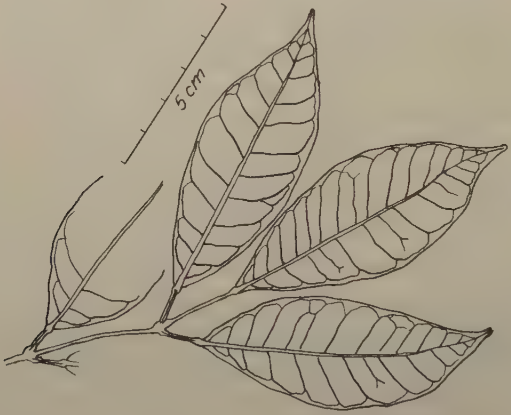

Fig. 3. *Protium dusenii* Swart—Dusén 15296 (K).

Protium fimbriatum Swart n. sp. Arbor usque ad 20 mm alta. Ramuli robusti angulosi cum petiolis petiolulis rachibusque dense ferrugineo-puberuli. Folia 6-juga 50 vel 65 cm longa, petiolis semiteretibus 17.5 (15–20) cm longis basi incrassatis adultis transverse rimosis, interjugis terete-striatis supra carinatis 3.5–4 (2.5–5) cm longis basalibus quam cetera plerumque brevioribus, petiolulis teretibus sulcatis transverse rimosis 5–7.5 mm longis foliolorum terminalibus teretis 25–30 mm longis, foliolis ovato-lanceolatis interdum oblongo-lanceolatis 20 (16–24) cm longis 6 (5.5–6.5) cm latis terminalibus brevioribus oblongis basalibus minoribus, apice gradatim acuminatis, acumine sublineari obtuso sexies longiora quam latiore 15–20 mm longo 2.5–3 mm lato, basi rotundo vel subemarginato, margine integro undulato subrepando, subcoriaceis scabridulis supra nitidis subtus opacis, nervis sec. utrinque 13–16 nervis prim. supra utrinque sulcatis glabris subtus valde prominentibus dense puberulis nervis sec. supra prominulis glabris subtus prominentibus sparse puberulis nervis tert. supra vix prominulis glabris subtus prominentibus pilis nonnullis munitis. Inflorescentiae pseudo-terminalis aut axillaris 15–20 cm longae ramuli sec. paucis divaricatis usque ad 7.5 cm longis ramulis tert. nonnullis usque ad 2 cm longis. Rhaches robustae angulosae dense ferrugineo-puberulae. Pedicelli teretes 2–3 mm longi cum bracteis bracteolisque triangularibus acutis 0.5 mm longis calycibus corollibusque sparse ferrugineo-puberulis. Flores 5-meri 3.5 mm longi. Calyx cupuliformis lobis late triangularius acutis tubo circiter aequilongis. Petala subinduplicativo-valvata oblongo-triangularia acuta carnosa apiculo inflexo incrassato. Stamina 10, in fl. masc. 2 mm longa, filamenta subulata antheris oblongis duplo longiora. Discus in fl. masc. cum pistillo rudimentario in globulum dense ferrugineo-pubescentem circiter 2 mm altum confluens, in fl. fem. annularis glaber sed margine distincte et densiuscule fimbriatus. Drupa obliquo-ovoidea et 1-pyrena aut 2- vel 3-loba et 2- vel 3-pyrena, dense ferrugineo-puberula basi lobata apice acuta stigmate distincte 5-lobo coronata 2 cm longa 1–2 cm diam., mesocarpio crassiusculo carnoso endocarpio tenuo lignoso fragilis.

Holotypus: Krukoff 7024 (U, 23190A).

BRAZIL, Amazonia, basin of Rio Madeira, near Calama, Krukoff 1308 (Dec. 1931, fruct.) (B, K, NY, U).; id., id., munic, Humayta, on river Livramento, Krukoff 7024 (Oct.–Nov. 1934, fruct. and fl. masc.) (K, U).

Protium fimbriatum Swart is near to *P. apiculatum* Swart, but differs by its 6-jugate, 50–65 long leaves and its leaflets with rotundate base and an acumen six times as long as wide, besides a fimbriate disc in the fem. flowers.

Protium firmum Swart n. sp. Arbor 25 m alta. Ramuli robusti 1 cm diam. teretes striati juveniles sparse ferrugineo-piloselli, adulti glabrescentes. Folia 6-juga interdum 7-juga, 60–65 cm longa, petiolis prope basim incrassatis semiteretibus 18 cm longis cum rhachibus petiolulisque pilis patentibus sed brevibus ferruginea obtectis, interjugis teretibus carinatis 5–6 cm longis basalibus quam cetera brevioribus, petiolulis teretibus canaliculatis adultis transverse rimosis 10–15 mm longis foliolorum terminalium teretibus 35 mm longis, foliolis lanceolatis vel lanceolata-oblongis nonnunquam basim versus angu-

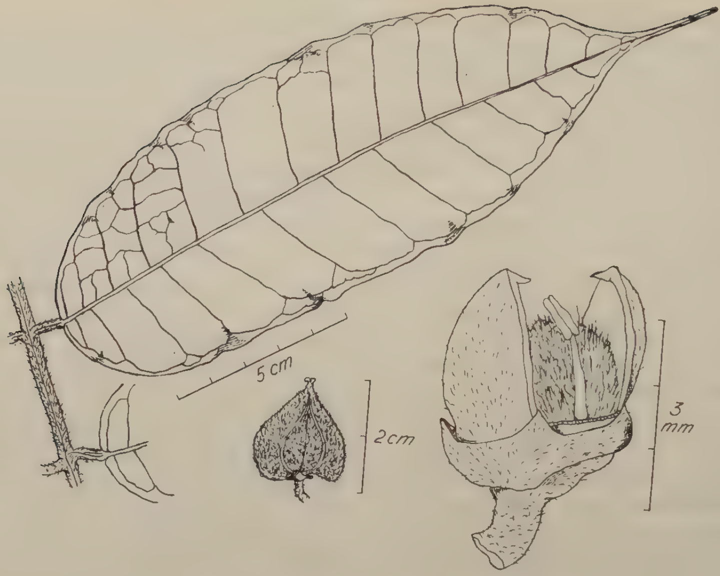

Fig. 4. *Protium fimbriatum* Swart—Krukoff 7024 (U).

statis 21 (18–25) cm longis 6 (5–7) cm latis sed foliolis terminalibus et foliolis jugi apicalis et jugi basalis minoribus 16 cm longis 5 cm latis, apice gradatim acuminatis, acumine attenuato obtuso longitudine latitudine aequantibus 5 mm longo, basi acute-cuneato, margine integro, subcoriaceis laevibus glabris supra nitidis subtus opacis, nervis sec. utrinque 14–15, nervis prim. et sec. prominentibus nervis tert. prominulis omnibus glabris costis facie inferiore sparse pilosellis tamen exceptis. Inflorescentiae in axillis solitariae 5–10 cm longae pedunculis robustis ramulis sec. paucis ad 0.5 cm longis. Rhaches robustae terete-striatae cum bracteis bracteolisque triangularibus 0.5 mm longis pedicellis teretibus 0.5–1.5 mm longis calycibus corollibusque facie exteriore sparse minute ferrugineo-pubsecentae. Flores in glomerula structura dichasialia congesti 5-meri 3 mm longi. Calyx cupuliformis 1 mm altus lobis late triangularibus acutis tube fere aequilongis. Petala elliptico-ovata subinduplicativo-valvata subcarnosa apice acuta inflexo-apiculata. Stamina 10 in fl. fem. 1.5 mm longa, filamenta subulata antheris oblongis bis longiora. Discus in fl. fem. annularus sparse puberulus margine fimbriatus 0.5 mm altus. Pistillum in fl. fem. densiuscule adpresse ferrugineo-puberulum 1.5 altum ovario ovoideo 5-lobo 5-loculari in stigma sessile 5-lobum attenuato.

Holotypus: Krukoff 7142 (U, 23315A).

BRAZIL, Amazonas, munic. Humayta, on plateau between Rio Livramento and Rio Ipixuna, Krukoff 1742 (Nov. 1934, fl. fem.) (K, NY, U).

Protium firmum Swart shows conformity with *Protium apiculatum* Swart, but the latter differs by the smaller, usually 3-jugate leaves, by the smaller, relatively broader and distinctly thinner leaflets with a mucronulate acumen twice as long as wide and by its much longer subterminal inflorescences.

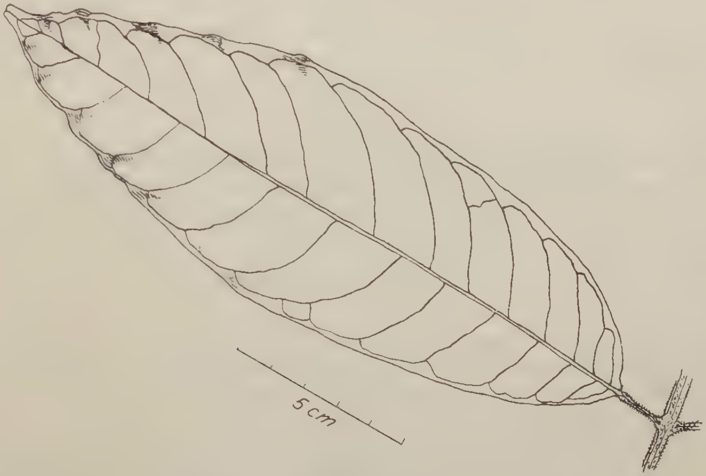

Fig. 5. *Protium firmum* Swart—Krukoff 7142 (U).

Protium glaziovii Swart n. sp. Arbor?. Ramuli robustini teretes luridi minute piloselli. Folia 3-juga interdum 4-juga 12.5 cm usque ad 17.5 cm longa, petiolis robustis semiteretibus 1.75 (1–2) cm longis cum interjugis petiolulisque costis foliolorum untrinque sparse et minutissime puberulis, interjugis teretibus supra carinatis 2.25 (1.75–2.75) cm longis, petiolulis semiteretibus sulcatis utroque extumo subincrassatis 0.5 cm longis sed foliolorum terminalibus 1-1.5 cm longis, foliolis oblongis 6 (4.5–7) cm longis 3 (2–3) cm latis terminalibus basim versus paulo angustatis lateralibus non angustatis aut apicem versus paulo angustatis basalibus brevioribus, apicem gradatim acuminatis, acumine attenuato obtuso bis longiore quam latiore 6 mm longo 3 mm lato, basi cuneatis, margine integro, pergamentaceis laevibus glabris supra subopacis subtus subnitidis, nervis sec. utrinque 11, nervis prim. prominentibus nervis sec. prominulis nervis tert. vix distinguendis. Inflorescentiae axillares laxe breviter ramosae petiolis foliorum suffulcientium usque ad bis longiores, rhachibus teretibus striatis sparse puberulis pedunculis usque ad 7 cm longis ramulis sec. ad 1 cm longis. Pedicelli teretes 1–2 mm longi cum bracteis bracteolisque triangularibus acutis 0.4 mm longis calycibusque densiuscule puberuli. Flores 4-meri 3 mm longi. Calyx cupuliformis 1 mm altus lobis triangularibus acutis tubo aequilongis. Petala oblongo-triangularia glabra apice acuto incrassato apiculo inflexo munito. Stamina 8 filamentis subulatis 1 mm longis antheris oblongis 0.75 mm longis. Discus annularus 8-lobus glaber. Pistillum in fl. masc. 1 mm altum ovario globoso 4-lobo dense puberulo stylo 0.5 mm longo stigmate 4-lobo coronato.

Holotypus: Glaziou 19014 (K).

Brazil, Rio de Janeiro, Glaziou 19014 (1892, fl. masc.) (B, C, K, LE, US).

Protium glaziovii Swart is in regard to the indumentum of its vegetative parts similar to *P. nicaraguense* Swart and to *P. hostmannii* Engl., but the fromer differs by its leaves being twice as large and by the acumen of the leaflets being 5-times as long as wide, and the latter species differs by its mostly 2-jugate leaves with larger leaflets and by its inflorescence at most as long as the petiole.

Protium hostmannii Engl. var. **brasiliense** Swart n. var. Folia 1-juga, petiolis interjugis petiolulisque minutissime puberulis, foliolis subcoriaceis nervis sec. vix prominulis acumine attenuato instructis.

Holotypus: G. A. Black 48–3613 (IAN).

Brazil, Amazonia, Para, Souve, Ilha do Marajo, G. A. Black 48–3613 (1948, fruct. Sept.) (IAN).

Protium paraense Swart n. sp. Arbor circ. 10 m alta. Ramuli graciles 2–3 mm diam. teretes striati luridi vel castanei, juveniles densiuscule longiuscule pilosi.

Folia 3- vel 5-juga plerumque 4-juga 20 (17–21) cm longa, petiolis semiteretibus 2 (1.5–2) cm longis cum interjugis semiteretibus carinatis 2.5 (2.25–3) cm longis petiolulisque densiuscule pilosellis pilis brevibus cum pilis aliquibus longioribus deciduis mixtis, petiolulis foliolorum lateralium teretibus sulcatis 2–3 mm longis foliolorum terminalibus teretibus 15 mm longis, foliolis lanceolatis vel oblongo-lanceolatis 8.5 (8–9.5) cm longis 2.25 (2–2.5) cm latis terminalibus paulo brevioribus basim versus distincte angustatis lateralibus interdum apicem versus paulo angustatis basalibus brevioribus, apice sensim in acumen lineare obtusum 10 mm longum 2 mm latum attenuatis, basi acute cuneatis, margine integro undulato, chartaceis utrinque laevibus opacis, nervis sec. utrinque 12 vel 14 nervis prim. utrinque prominentibus nervis sec. supra conspicuis infra prominulis nervis tert. supra inconspicuis infra conspicuis nervis prim. et sec. densiuscule pilosellis. Inflorescentiae axillares glomeruliformes 1 cm diam. multiflori, rhachibus teretibus cum pedicellis teretibus striatis 1–1.5 mm longis bracteis bracteolisque triangularibus acutis 0.5 mm longis densiuscule pilosellis. Flores 4-meri 3 mm longi glabri. Calyx cupuliformis 1 mm altus lobis triangularibus acutis tubo longioribus. Petala induplicativo-valvata ovata acuta apiculo incrassato inflexo. Stamina 8 circ. 2 mm longa filamentis subulatis antheris ellipticis 0.5 mm longis. Discus annularis 8-lobus 0.5 mm altus. Pistillum in fl. masc. disco immersum 0.5 mm altum, ovario late ovoideo 4-sulcato in stigma sessile 4-lobum attenuato.

Holotypus: Inst. Argon. do Norto Registro 210 (IAN).

Brazil, Amazonia, Belem, Bosque Municipal, Inst. Agron. do Norte Registro 210 (fl. masc.) (IAN).

Protium paraense Swart resembles *P. trifoliolatum* Engl., but differs by its 4-jugate leaves with short petiolules and lanceolate leaflets with a narrower acumen and more numerous pairs of sec. nerves.

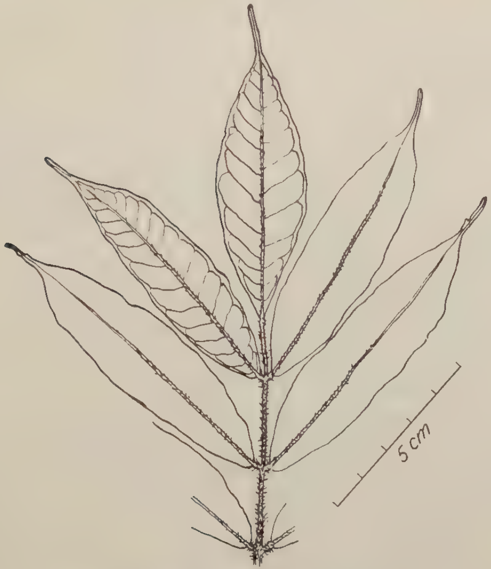

Fig. 6. *Protium paraense* Swart—IAN Registro 210 (IAN).

Protium piresii Swart n. sp. Arbor. Ramuli teretes striati 3 mm. diam., juveniles sparse ferrugineo-piloselli, demum glabrescentes fulvi. Folia 2- vel 3-juga 15–18 cm longa, petiolis semiteretibus 2.5–3.5 cm longis cum rhachide petiolulis costis foliolorum facie superiore pilis patentibus densiuscule sed brevissime vestitis, interjugis terete-carinatis apicem versus bisulcatis 2.5–3.5 cm longis, petiolulis semiteretibus sulcatis utroque extremo subincrassatis 5–6 mm longis sed petiolulis foliolorum terminalium teretibus 20 mm longis, foliolis oblongis 7.5 (7–9) cm longis 2 (2.75–3.5) cm latis, terminalibus paulo latioris prope basim angustatis, lateralibus plerumque e medio apicem versus paulo angustatis, apicem versus sensim acuminato, acumine sublineari obtuso 10 mm longo 2 mm lato, basi cuneatis, margine integris, pergamentaceis laevibus glabris utrinque opacis, nervis sec. utrinque 10, nervis prim. prominentibus supra sparse minutissime pilosis infra glabris nervis sec. glabris supra prominulis infra prominentibus nervis tert. conspicuis. Inflorescentiae axillares e basi ramosae 5–7 cm longae ramulis sec. ad 2 cm longis rhachibus angularibus cum pedicellis angularibus 1 mm longis sparse pilosellis. Flores 4-meri 3 mm longi. Calyx cupuliformis 0.5 mm altus glaber lobis triangularibus acutis tubo aequilongis. Petala oblongo-triangularia acuta apiculo acuto inflexo instructa glabra margine papillosa. Stamina 8 filamentis subulatis antheris oblongis subaequilongis. Discus annularis glaber 0.5 mm altus. Pistillum in fl. masc. disco cintum fere 1 mm altum, ovario ovoideo 4-lobo pilis minutis obtecto, stylo brevi, stigmate 4-lobo.

Holotypus: Pires 2693 (IAN).

Brazil, Amazonia, Para, Belem, Aura. Pires 2693 (1950, fl. masc. Nov.) (IAN).

P. piresii Swart resembles *P. hostmannii* Engl. but the latter differs

by its petiole being shorter than the interjugum, by the acumen of the leaflets being only 2- to 3-times as long as wide and by its glomeruliform inflorescences.

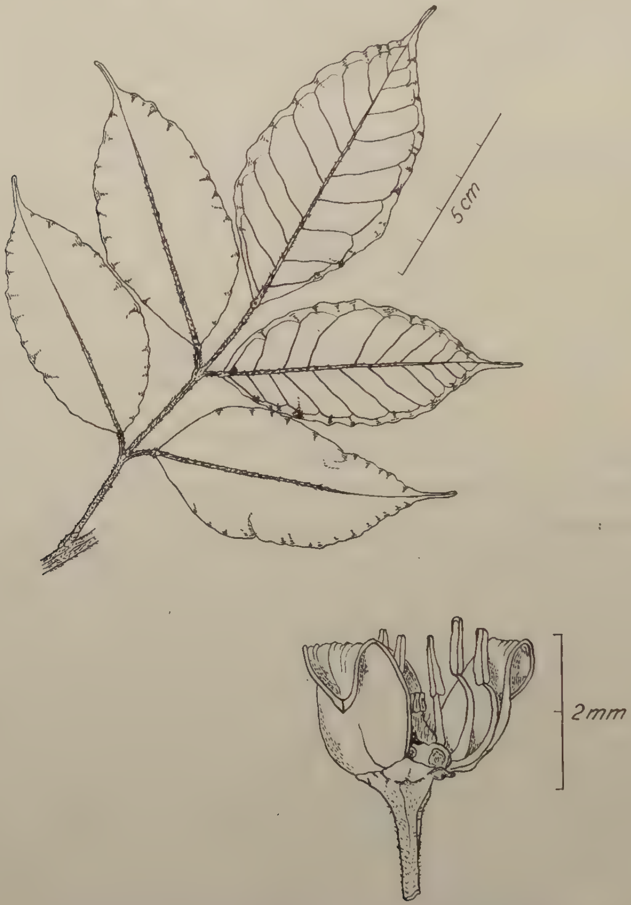

Fig. 7. *Protium piresii* Swart—Pires 2693 (IAN).

Protium polybotryum (Turcz.) Engl. var. **blackii** Swart n. var. Folio minora 20–30 cm longa graciliora, foliolis lanceolatis vel lanceolato-oblongis 9.5 (7.5–10.5) cm longis 2.5 (2.25–2.75) cm latis. Inflorescentiae longiores quam dimidia pars folii suffulcientis.

Holotypus: G. A. Black 49–8085 (IAN).

Brazil, Amazonia, Para, Belem, Mocambo, G. A. Black, 49–8085 (1949, fruct. July) (IAN).

Protium polybotryum (Turcz.) Engl. var. **robustum** Swart n. var. Petioli rhaches petioluli pedunculi robusti. Folioli acumen circ. quater longius quam latius, 6–8 mm longum 1.5–2 latum. Inflorescentiae in axillis solitariae.

Holotypus: Brit. Guiana Record no. 3140.

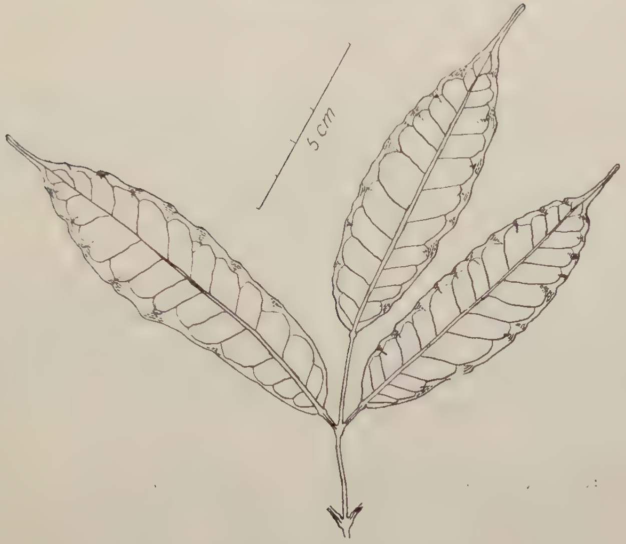

Fig. 8. *Protium polybotryum* (Turcz.) Engl. var. *blackii* Swart—Black 49–8085 (IAN).

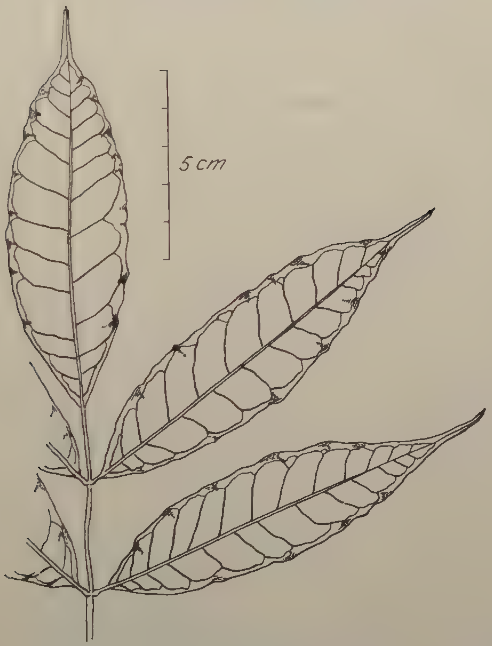

Fig. 9. *Tetragastris panamensis* (Engl.) O.K. var. *grandifolia* Swart—Lindeman 5052 (U).

British Guiana, Demerara-river, Hibibia-creek, Record no. 3140 (1940, fruct. March) (K).

Vern. name: purokai.

Tetragastris panamensis (Engl.) O. K. var. **grandifolia** Swart n. var. Folio 4- vel 5- (3- vel 7-) juga 40–50 (35–60) cm longa, petiolis 12–16 (10–20) cm longis, interjugis 4–7 (2.5–8) cm longis basalibus 3–5 (2–7) cm longis, foliolis oblongo-lanceolatis 15 (9.5–23) cm longis 4.5 (3–6.5) cm latis, nervis sec. utrinque 11–15.

Holotypus: Lindeman 5052 (U, 078233B).

Suriname, slopes of Nassau-mountains, Lanjouw and Lindeman, 2543 (1949) (U); between Suriname-river and Mapane-creek, Lindeman 3659 (1953) (U); id., id. 3736 (1953) (U); id., id. 3748 (1953) (U); id., id. 3776 (1953) (U); id., id. 5038 (1953) (U); id., id. 5039 (1953) (U); id., id. 5052 (1953) (U); type; Moengo-tapoe, Rikanau, Lindeman, 5905 (1954) (U); between Suriname-river and Mapane-creek, Lindeman 6747 (1954) (U).

Vern. name: salie

Trattinickia burserifolia Mart. var. **lindemanii** Swart n. var. Folia magna 40–50 cm longa, petiolis 8–11 cm longis, interjugis 5–8 cm longis, petiolulis 1–2 cm longis, foliolis usque ad 18 cm longis interdum apicem versus paulo angustatis acumine bis longiore quam latiore.

Holotypus: Lindeman 4525 (U, 078243B).

Suriname, south of Paramaribo, near Lelydorp, Lindeman 4525 (1953 Aug., fl. buds) (U); Moengo-tapoe, Rikanau, Lindeman 6117 (1954) (U).

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SOME REMARKS ON THE TAXONOMY OF CYANOPHYCEAE

JOSÉPHINE TH. KOSTER

(Rijksherbarium, Leiden)

(received October 6th, 1965)

Together with the class of the *Schizomycetes* (bacteria) the *Cyanophyceae* belong to the division of the *Schizophyta* which division differs from all other plant divisions by lacking a nucleus. However, the central part of their cells is a nuclear equivalent (Procaryota). This nucleoplasm or centroplasm or central body in the *Cyanophycean* cell has been studied profoundly these last fifteen years (Beck, Bowen, Cassel, Fuhs, Giesy, Herbst, Hutchinson, Jensen, Jost, Pankratz, Rabinovich, Sun and others) by means of the electron microscope. The resulting papers are mostly beautifully illustrated by electron micrographs. Pure cultures of *Chroococcales* (*Gloeocapsa*, *Gloeothece*, *Pleurocapsa*) as well as *Hormogonales* (*Anabaena*, *Nostoc*, *Microcoleus*, *Oscillatoria*, *Phormidium*, *Symploca*) have served for these investigations. The general results of these studies have provided us with a detailed picture of the nucleoplasm. The uncoloured nucleoplasm often has a fine reticulate-fibrillar texture, the anastomosing fibrils are intertwined by cytoplasm. In the nucleoplasm have been found to occur: vacuoles, opaque globular granules and polygonous bodies, which have a connection with the reticulate structure. Though the nucleoplasm contains nuclear material, the general conclusion is that there are no chromosomes and that no mitosis occurs. Only Fuhs (1958), who discovered Feulgen-positive linear filiform or bar-shaped structures in the centroplasm, about 0.2 μ in diameter, compared these with chromosomes, for their length is more or less constant and they split longitudinally into two diverging parts. He did not see any spindle-shape, however, inherent to mitosis. Cassel and Hutchinson (1954) doubt the possibility of a comparison with chromosomes since the resembling structures vary in shape and size in various cells.

Several former investigators were positive about the existence of a true nucleus and chromosomes in the cell of *Cyanophyceae*. Kohl (1903) wrote a book about: "Organisation und Physiologie der Cyanophyceenzelle und die mitotische Teilung ihres Kernes", in which numerous coloured figures show the mitosis and the chromosomes, observed with a light microscope. *Tolypothrix lanata* was used for these studies. Kohl did not see a nuclear membrane. To-day, investigators who have made electron-microscopic studies are convinced that no such a membrane between nucleoplasm and chromoplasm exists. They, however, do not at all confirm those bold conclusions concerning chromosomes and mitosis. Cell-division starts with an annular constriction of the protoplast.

The wall of the *Cyanophycean* cell consists of two, three or four layers. In the *Hormogonales* are found to occur fine connections through the cell-wall between the protoplast of two neighbouring cells. Inside the cell-wall is the coloured part of the cytoplasm, the chromo- or chromatoplasm, having lamellar structures to which chlorophyll and photo-synthesis are inherent. Also vacuoles and cyanophycine-granules occur in the chromoplasm.

The *Cyanophyceae* differ from the bacteria according to FOTT, 1950 (pp. 27, 40) by never having moving flagellate cells and often having hormogonal, but never simple trichomes and by in many cases showing hormogonal movements. Consequently, like others, this author considers *Beggiatoa* and *Thiothrix* to belong to the *Cyanophyceae*, for these organisms have hormogonal trichomes and *Beggiatoa* shows *Oscillatoria*-like movements, *Thiothrix* forms hormogones. In Fott's opinion, the lack of photosynthetic pigments in such apochlorotic genera, as are *Beggiatoa* and *Thiothrix*, is an unreliable character, since many *Cyanophyceae* are only faintly coloured or nearly colourless and bacteria can be green or purple coloured. SORIANO and LEWIN (1965) are of an opposite opinion. They deem the occurrence of the sulphur granules in the *Beggiatoa* cells, though rarely lacking, to be an important character and do not think it appropriate to place that genus in the *Oscillatoriaceae* nor in the *Beggiatoaceae* in the *Hormogonales*. They consider *Beggiatoa* to belong to the *Flexibacteria*. These authors indicate that there are numerous one- or more-celled apochlorotic gliding organisms without flagella, related to the *Cyanophyceae* but having no photosynthetic pigments, living in marine as well in freshwater habitats. Many of these organisms have been described originally as *Oscillatoria* species. There are gradual transitions from the above mentioned organisms to *Myxobacteria*. Soriano and Lewin conclude that there is no natural limit between the *Cyanophyceae* and the bacteria. Physiologally, as they indicate, there is some difference, since the *Cyanophyceae* possess chlorophyll a and evolve oxygen, whereas the bacteria generally are not photosynthetic and if so, do not evolve oxygen. After considering the above mentioned arguments, we may agree that no natural limit exists between the *Cyanophyceae* and the bacteria. In a recent paper ECHLIN and MORRIS (1965), after thorough considerations, came to the suggestion that "bacteria and blue-green algae should be isolated in a group distinct from all other organisms."

Despite the sharp delimitation of the *Cyanophyceae* from the other classes of algae, they are readily, also in the latest works on classification (FOTT, 1959; CHRISTENSEN, 1964) placed among the *Algae*. In fact, the shape of the cells and of the colonies of several Cyanophycean species show a great resemblance to those of Chlorophycean species. Difficulties are met with in delimitation of the genera and the species of the *Cyanophyceae*. The morphological variability, as well as the differences caused by various environmental conditions and the different stages in growth, all suggest different species thus causing these difficulties. For this reason it is advisable, not to describe a new Cyanophycean species just because the material concerned is not identical with the species to which certain keys for identification lead or with descriptions in flora's, however good these may be. Finding in PANKOW and JAHNKE (1965, p. 332): "*Oscillatoria lutescens* nova spec. Eine am 27 Oktober 1963 aus einem Dorfteich in Dummerstorf (bei Rostock) entnommene Wasserprobe enthielt reichlich farblos-gelblichgrüne Trichome einer *Oscillatoria-Art*, die sich mit Hilfe der gebräuchliche Bestimmungsschlüssel (GEITLER, 1932; DESIKACHARY, 1959) nicht bestimmen liess", or in WELSH (1964, p. 258) concerning *Oscillatoria Chutteri* n. sp. "It will be seen from this diagnosis and the iconographs that this alga has certain features reminiscent of *Oscillatoria Martini* Frémy, *O. janthiphora* (Fior.-Mazz.) Gomont, *O. leatevirens* (Crouan) Gomont, *O. acuminata* Gomont, *O. brevis* (Kütz.) Gomont, and *O. Boryana* Bory ex Gomont, and of *Phormidium favosum* (Bory) Gomont, *Ph. subfuscum* Kütz. ex Gomont, *Ph. uncinatum* Gomont, and *Ph. autumnale* (Ag.) Gomont, but none of these ten species possesses all the features and measurements of the present one" we hardly feel convinced that these species are new species. For, to discover whether a species is really a new one a thorough study is required not only of the genus concerned but also of the related ones to obtain an understanding of their variability. This must be done both by studying the literature and also by studying a good quantity of material. Now that cultures of *Cyanophyceae* with hardly any bacterial contamination can be obtained by using ultraviolet radiation, they certainly are very useful to complete such a study of dried specimens and material preserved in liquid, as long as abnormal forms which sometimes appear in cultures are duly recognized.

To make the publication of a new Cyanophycean species valid the nomenclatural type should be dried material and not a mere figure. Dried material of *Cyanophyceae* can, in most cases, be satisfactorily studied after being soaked in dilute detergent.

Variability in the *Cyanophyceae*, not only in morphology but also occurring in different circumstances and in different stages of the species has been demonstrated already by CROW (1923, 1924) by means of experiments. Yet, he did not go as far as changing the existing concept of the species of the *Cyanophyceae* with this knowledge. For, in his study of *Microcystis* (1923) in spite of his statement: "whenever abundant material occurs the precise limits of the different species become impossible to define" and discovering intermediate forms between the species in one and the same environment, he gives a key for 17 species, which he himself judges to be artificial.

Variability in *Cyanophyceae* was also demonstrated by JAAG's (1945) experiments with a not definitively identified *Scytonema*. The light intensity appeared not only to influence the colour and the habit of the colony, but also the false branching which could be single, double or wanting, as well as the occurrence of heterocysts which could be more or less abundant or wanting. The number and occurrence of the false branches, as well as the occurrence of the heterocysts are important characters to distinguish genera and families in the *Cyanophyceae*. A similar result was obtained by STEIN (1963) from her cultures of a *Tolypothrix* species, finding forms with single and forms with double false branches.

In nature, JAAG (1943) discovered the great variability in the sheath and the false branching of *Scytonema myochrous*, with status crustaceum in extreme dry places, status myochrous in moist habitats and status petalonema in very wet places. Up to that time the three states were considered to be three species: *Scytonema crustaceum*, *Scytonema myochrous* and *Petalonema alatum*, but Jaag discovered intermediate forms. The present author recently collected the same species on a moist east-exposed rock-wall with rare, very short, nearly all single false branches.

SCHWABE (1964) in one of his last papers, carefully avoided a definitive delineation of *Oscillatoria acutissima* Kuff. feeling that a better knowledge of the variability is required.

Unbranched filaments are characteristic for the genus *Lyngbya*, but in *Lyngbya aestuarii* occasionally false branching occurs (GOMONT, 1892, p. 149; KOSTER, 1960, p. 359, fig. 44).

CROW's (1924, p. 407) remark: "The old idea that the naturally occurring forms of *Cyanophyceae* are numerous polymorphs of a few main types, receives no support from modern systematists" could not be written in these days, since DROUET and DAILY's (1956) and FAN's (1956) revisions of Cyanophycean genera and DROUET's papers on polymorphous Cyanophycean species (1962, 1963, 1964) appeared. For the time being, the changes of more or less well known names of genera and species or placing them into the synonymy of other species, which appeared to be necessary from these revisions, cause certain difficulties and annoyance for many phycologists, such as ecologists, cytologists, physiologists. It is natural that only gradually will the change of names as indicated in the revisions find their way into the phycological papers. Confusing, however, are motiveless alterations of descriptions of species such as in the interesting paper of GIESY (1962, p. 122), where *Oscillatoria limosa* Agardh is indicated to have trichomes which are 2–6 μ in diameter. *O. limosa* Ag. ex Gom., a characteristic species, is described by GOMONT (1892, p. 211) as having trichomes which are 11–20 (usually 13–16) μ in diameter.

In extremely variable species it may be of interest to distinguish infraspecific entities, sometimes for convenience' sake rather than of taxonomic value, such as varieties, formae, formae speciales, ecophenes and status indicating minor differences, like in *Lyngbya aesturarii* (Mertens) Liebm. ex Gom. (Gomont, p. 149, 150) and in *Mastigocladus laminosus* Cohn ex Kirch. (syn. *Hapalosiphon laminosus* Hansgirg ex Born. et Flah.) as described by several authors and recently by *Anagnostidis* (1961, p. 109, p. 279–281).

This paper was written in honour of Dr. J. Lanjouw who has been teaching general plant taxonomy at the Rijksuniversteit of Utrecht for about 35 years. May he find some interest in these remarks about one of the oldest groups of plants, being recorded already from Precambrian, Cambrian, Silurean and Devonian formations.

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THE GENUS CLUSIA (GUTTIFERAE) IN SURINAME

BASSETT MAGUIRE
(New York Botanical Garden)

(received October 23rd, 1965)

The precursor studies[1]) and floristic treatment of P. J. Eyma of the Guttiferae of Suriname[2]) exhibited a remarkably keen insight into the biology and taxonomy of this rather complicated family. Particularly this is true of the genus *Clusia*, which is the concern of this paper, and for which even yet the overall biology is indeed too little known.

In the Flora of Surinam (l.c.) Eyma admitted eleven species. Now, as a result of more field activity from which much new material has been derived, there can be credited to Suriname fourteen species, of which three have been collected in that country subsequent to the studies of Eyma. Name changes are required for two species.

In this paper new keys are provided, based separately upon flowering and fruiting materials of both male and female plants, and pertinent notes are offered which are intended to supplement the account of Eyma. For five species descriptions which are lacking in the Eyma treatment, or require restatement, are herein provided.

Materials employed in the preparation of this account have kindly been made available by the following herbaria: BR, F, G, GH, K, NY, P, U, US and W.

Keys to the Species of the Genus Clusia of Suriname Based Separately on Pistillate and on Staminate Materials

I. *Key to Clusia of Suriname, pistillate*

1. Stigmas borne on evident styles.
    2. Styles 16, filiform, 3–6 mm l; ovaries and fruit 16-celled; *Sect. Clusiastrum.*
        3. Sepals commonly 7–10; inflorescence commonly 3- or more-flowered; lamina commonly 20–40 cm l, broadly ovate to obovate; petioles 1.5–3.0 cm l, winged. . . . 1. *Clusia stylosa*
        3. Sepals 12–14; inflorescence commonly 1-flowered, sometimes 3-flowered; lamina commonly 10–16 cm l, elliptic, sessile . . . . 2. *Clusia tabulamontana*
    2. Styles 5 (4–6), stout, cornute, ovaries and fruit 5 (4–6)-celled, each cell several-seeded; sepals 4, petals commonly 5; staminodia lacking; *Sect. Anandrogyne* . . . . . . 3. *Clusia sessilis*

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[1]) Eyma, P. J. 1932. New and critical Polygonaceae, Guttiferae and Lecythidaceae from Surinam, Meded. Bot. Mus. Herb. Univ. Utrecht No. 4: 6–46.

[2]) Eyma, P. J. 1934. Guttiferae in Pulle. Fl. Surinam **3**: 65–118.

1. Stigmas not borne on evident styles, hence essentially sessile.

4. Ovary and fruit 4(5)-celled; capsule 6–15 mm l, each cell commonly 1-seeded; lamina oblong-obovate or broadly obovate to 20 cm l, latex whitish; *Sect. Criuva* . . . 4. *Clusia melchiori*

4. Ovary and fruit 5-celled.

5. Ovary subtended by 5–10 stout essentially free staminodia; latex white or whitish.

6. Staminodia 5, sterile, devoid of anthers; capsule obovate-turbinate, 8–14 mm l, commonly strongly transversely rugose, each cell 3–6-seeded; petioles slender, 5–15 mm l, lamina obovate to oblanceolate, (3)8–12 cm l; latex clear; *Sect. Pseudo-quapoia* 5. *Clusia pana-panari*

6. Staminodia or stamens 10, each bearing a terminal circular embedded usually functional anther; flowers apparently ⚥; ovary and fruit 5-celled; stigmas deltoid, at length 8–10 mm l, dimpled; petiole short, winged, lamina obovate-cuneate, to 20 cm l; latex yellowish, oxidizing red; *Sect. Polythecandra* . . . . . 6. *Clusia scorbiculata*

5. Ovary subtended by a discoid or cupuliform, commonly sterile, synandrium, or synandrium-like body.

7. Synandrium (if indeed a synandrium obtains) unknown, but possibly of discrete prismatic staminodia; sepals probably 7–9, the upper imbricate and broadly scarious-margined; capsule pentagonal to 5 cm l, strongly transversely rugose; *Sect. Phloianthera* . . 7. *Clusia purpurea*

7. Synandrium or synandrium-like body provided with staminodia; capsule neither pentagonal nor rugose.

8. Ovules and seed commonly 1 in each cell; staminodia muticous, in several rows, adherent in a low ring 1.5–2.0 mm h; fruit flask-shaped; stigmas 5, ca. 2 mm l, sharply connivent; leaf-apex more often abruptly apiculate or shortly acuminate; latex white; *Sect. Androstylium* . . . . 8. *Clusia fockeana*

8. Ovules and seed commonly several in each cell; staminodia in several rows, flat, linear, awned, antherous, glutinous, borne on a corona ca. 5 mm h; fruit oblong-ellipsoid, to 3 cm l; stigmas 5–8, ca. 3 mm l, more or less spreading, not sharply connivent; leaf-apex more often acute or obtuse; latex yellowish; *Sect. Clusia* . . . . 10. *Clusia nemorosa*

4. Ovary and fruit more than 5-celled.

9. Ovary 6–8-celled, with 6–8 stigmas.

10. Staminodia lacking, or if provided with stamens the anthers fertile and the flowers ⚥; stigmas upturned, radiate; leaves subsessile or with petioles 1–2 cm l, lamina cuneate-obovate, obtuse, commonly latex canals prominent; latex white; *Sect. "Minor"* 9. *Clusia minor*

10. Staminodia numerous, plane, several-ranked, awned, anantherous, glutinous; cells of ovary 6–8, sometimes

only 5; stigmas ascending; petioles 2–3.5 cm l, lamina elliptic or obovate-oblanceolate, commonly 10–15 cm l, latex yellow; *Sect. Clusia* . . . . 10. *Clusia nemorosa*

9. Ovary 10- or more-celled, stigmas 10 or more; latex yellow; *Sect. Clusia.*
    11. Fruit depressed-globose, without gynobase; younger internodes coarse, commonly 1 cm more thick.
        12. Ovary 12–16-celled; stigmas 12 or 16, forming a thick, broad, umbraculiform adpressed cap; fruit depressed-globose to 10 cm diam; younger internodes decussately angled . . . . . 11. *Clusia grandiflora*
        12. Ovary 12–14-celled; stigmas 12–14, flat, not elevated; fruit depressed-globose to 6 cm diam; younger internodes terete . . . . . . 12. *Clusia platystigma*
    11. Fruit ovate-globose; branchlets terete.
        13. Ovary and fruit 10-celled, the fruit deeply sulcate, the stigmas capitate, 15–18 mm broad; leaf-blades obovate to orbicular-obovate, to 20 cm l, the base more or less abruptly rounded; bracts and bracteoles ovate-navicular, 1–1.25 cm l; commonly a small tree . . . . 13. *Clusia robusta*
        13. Fruit to 6 cm l, often provided with an obvious gynobase; stigmas capitate, 6–8 mm broad; branchlets slender, 8 mm or less thick; commonly an epiphyte . . . . 14. *Clusia palmicida*

II. *Key to Clusia of Suriname, staminate*

1. Flowers unisexual (occasionally staminodia may be fertile or partially so, cf. *Cl. purpurea* and *Cl. scorbiculata*), staminate, with or without rudimentary pistils.
    2. Stamens indefinite in number, much exceeding 10; filaments free to the base; anthers linear, 2-celled; rudimentary pistils lacking.
        3. Sepals 7–14, imbricate, only the lower opposite; petals 7–8, obovate, ca. 3 cm l, white; anthers dehiscing laterally towards the apex; latex white; *Sect. Clusiastrum.*
            4. Sepals 7–10; inflorescence (3) 5–15-flowered; lamina commonly 20–40 cm l, broadly ovate to obovate; petioles 1.5–3.0 cm l, winged . . . . . 1. *Clusia stylosa*
            4. Sepals commonly 12–14; inflorescence 1–3 (5)-flowered; lamina commonly 6–10 cm l, elliptic, sessile . . . . 2. *Clusia tabulamontana*
        3. Sepals 4 (bracteoles 4), decussate.
            5. Petals (4) 5, elliptic-oblong, 18–22 mm l, greenish-yellow or whitish, stamens ± 100, 8–12 mm l, inflorescence 3–5-flowered, flowers fragrant; leaves sessile, lamina broadly to narrowly lanceolate, commonly 10–25 cm l; latex white; *Sect. Anandrogyne* . . . 3. *Clusia sessilis*
            5. Petals 4, elliptic-oblong, 5–6 mm l, greenish-yellow;

stamens 16–20, free, 3.0–4.5 mm l; inflorescence many-flowered; petioles 5–18 mm l, lamina oblong-obovate or broadly obovate, to 20 cm l; latex white; *Sect. Criuva* . . . . 4. *Clusia melchiori*

2. Stamens indefinite or definite in number, aggregated, variously coalesced, or the filaments connate into a ring or corona at the base; rudimentary pistils sometimes present.

6. Stamens forming a synandrium, or aggregate synandrium-like central mass.

7. Androecium subglobose or globose; a central rudimentary pistil more often lacking.

8. Stamens commonly 15–25, forming a compact subglobose mass; filaments prismatic, stout, anthers distally lateral, opening by two terminal pores; latex clear; *Sect. Pseudo-quapoia* . . 5. *Clusia pana-panari*

8. Stamens numerous, forming a columnar androecium surmounted by a globose synandrium, the base of the column subtended by numerous staminodia, these often anther-bearing; petioles 1.5–4 cm l, lamina elliptic, oblong-obovate or rarely lanceolate, abruptly and often obliquely apiculate or short acuminate; latex white; *Sect. Androstylium* . . . . 8. *Clusia fockeana*

7. Androecium cupuliform or connate, enclosing or surrounding a rudimentary (sometimes well developed) pistil.

9. Anthers numerous, 2-celled, synandrium truncate-conical, 1.0–1.5 cm h; pistil probably often functional; sepals 7–9, broadly obovate, to 2 cm l, the lower pair opposite, the upper imbricate, all strongly scarious-margined; leaves subsessile; lamina oblong-obovate or oblong-cuneate, to 20 cm l; latex white; *Sect. Phloianthera* . . . . 7. *Clusia purpurea*

9. Anthers l-celled, saccate, annuliform, embedded in circular apical pits; filaments few, 1 (2)-ranked, massive, prismatic, cupuliform and connate at the base, ca. 1 cm h; flowers ⚥; leaves subsessile; blades obovate-cuneate to 20 cm l; latex yellowish, oxidizing red; *Sect. Polytheca* . . 6. *Clusia scorbiculata*

6. Stamens forming neither a synandrium nor an aggregated body; filaments distinct and free but connate at the base into a distinct collar or corona surrounding a central sterile depressed glutinous mass; latex yellow; *Sect. Clusia*

10. Petals 4–5, the blade white, 2–3 cm l, the claw red-purple or pink within; characteristically a shrub or tree . . . . 10. *Clusia nemorosa*

10. Petals 7–8, panduriform, white, flushed within with red or pink; commonly 5 cm or more l.

11. Branchlets coarse, 1 cm or more diam, decussately

angled . . . . 11. *Clusia grandiflora*

11. Younger internodes terete.
    12. Branchlets coarse, 1 cm or more diam.
        13. Anthers with connective produced as a flat narrowly acute appendage; lamina obovate to cuneate-obovate, to 25 cm l, gradually narrowed toward the base; bracts and bracteoles large, suborbicular 1.5–2.5 cm l; commonly a small tree . . . . 12. *Clusia platystigma*
        13. Anthers muticous; lamina obovate to orbicular-obovate, to 20 cm l, the base more or less abruptly rounded; bracts and bracteoles ovate-navicular, 1–1.25 cm l; commonly a small tree . . . . . 13. *Clusia robusta*
    12. Branchlets relatively slender, 5–8 mm diam; anthers with connective produced as a conspicuous slender awn; bracteoles small, triangular-ovate, acutish to acuminate, to 5 mm l; commonly an epiphyte . . . 14. *Clusia palmicida*

1. Flowers hermaphroditic (often wholly pistillate, then lacking either stamens or staminodia); stamens usually fertile, sometimes anantherous; leaves subsessile or with petioles to 1 cm l, lamina obovate-cuneate to obovate-rhombic, obtuse, 5–14 cm l; latex canals prominent; latex moderate, white . . . . . . 9. *Clusia minor*

1. **Clusia stylosa** Maguire, Bull. Torrey Club 75: 419, fig. 18, 1–6. 1948. Sect. Clusiastrum Pl. & Tr.

Shrub or tree to 10 m high, with scanty white or cream latex; branchlets coarse, more or less terete, little or not at all angled. Leaves (15) 20–40 cm l, (8) 10–15 cm w, coriaceous, broadly obovate to oblanceolate, rounded, from above the middle the blade gradually narrowed to the base; the petioles 1.5–3.0 cm l, broadly winged and frequently subauriculate, hence the leaves appearing sessile; the midrib not prominent above, strongly so, elevated and rounded below, the primary nerves prominent below, less so above, 8–10 mm apart, ascending in a 20° angle and collected in a peripheral vein 3–4 mm from the blade margin, secondary veins only a little less prominent. Inflorescence compact, 3–15-flowered, peduncle stout, 3–8 cm l, primary bracts 1.5–2.2 cm l, obtuse, secondary bracts usually ca. 8 mm l, obtuse or apiculate, the ultimate 5–6 mm l.

♂ flowers: sepals 7–10 imbricate or subdecussate, concave, suborbicular, margins scarious, to 1.5 cm long; petals 7–8 obovate, ca. 3 cm l, white; receptacle plane or somewhat convex; stamens numerous, considerably exceeding 100, free, 4–5 mm l, filaments slender ca. 1.5–2.0 mm l, anthers linear, dehiscing laterally and distally for ca. 1.5 mm, tardily or characteristically not dehiscing for their entire length; rudimentary pistil lacking; pollen 3-colporate, sphaeroid-deltoid, essentially isolateral, in equatorial view 27–32.2 μ diam.

♀ flowers: sepals usually 10, essentially imbricate, the outer paired; petals not observed; staminodia anantherous, free, numerous, 4–5 mm l, linear, 5–6-serial, borne on a low corona ca. 1 mm h; ovary 16-celled, ovules numerous, biseriate, axial, sessile; fruit oblong, narrowed at the summit into a crateriform beak 2–4 mm l, styles 16, free, 3–5 mm l, radiate, stigmas subbasally sessile, obovate, ca. 1 mm l; mature fruit probably exceeding 3 cm in length.

Distribution: Suriname.

Tafelberg: Common, *Clusia* bush, line between Savanna VIII and southwest escarpment, Sept. 5, 1944. *Maguire 24625* ♀ (holotype NY); common, *Clusia* bush, Savanna VIII, *Maguire 24626* ♂, *24545* ♂; Arrowhead Basin, *Maguire 24508* ♂. Emma Keten: forest on E. slope of Hendriktop below the top, dominated by this species, Aug. 17, 1959. *Daniëls & Jonker 960* ♂. Wilhelmina Gebergte: Frederik Top at 1050 m, Aug. 22, 1963. *Irwin et al. 54951* ♀.

Clusia stylosa and the next, *Cl. tabulamontana*, both of the Sect. *Clusiastrum*, were initially found on Tafelberg. Now they both have been collected on the high portion of the Wilhelmina Mountains, and the first also on Emma Keten, thus enlarging the record of their respective ranges to the adjacent lofty crystalline mountain masses of central Suriname. Otherwise, the ten members of the *Clusiastrum* are known only from the areas of the Roraima Formation, except for Tafelberg, in the Guayana Highland of Venezuela and contiguous British Guiana, Brazil and Colombia.

Members of the *Sect. Clusiastrum* are well set off from the other sections of *Clusia* by the broadly based subsessile or sessile leaves, white latex (oxidizing cream or yellowish), numerous imbricated sepals, free numerous stamens, with anthers dehiscing laterally and subapically, styles filiform, free (except in *Cl. cuneata*), and multicelled ovaries varying from 8 to 16 (in ours 16). The two Suriname species between themselves are readily recognized by leaf distinction alone. Flower differences are manifest.

2. **Clusia tabulamontana** Maguire, Bull. Torrey Club 75: 420, fig. 18, 7–10. 1948. Sect. Clusiastrum Pl. & Tr.

Shrubs or trees 5–7 m h, with scanty white or cream latex; branchlets coarse, more or less terete, little or not at all angled. Leaves 10–16 cm l, 5–7 cm w, coriaceous, elliptic, broadly obtuse at the apex, little narrowed at the base, essentially sessile, or a broad petiole hardly evident; the midrib depressed and not prominent above, elevated and rounded below, the primary nerves prominulous below, ascending at a 40° angle, 4–8 mm apart, collected in a peripheral vein 3–4 mm from the blade margin. Inflorescence 1–3-flowered, peduncle to 6 cm l and 5 mm diam; primary bracts obtuse, 1 cm l, secondary bracts 3–5 mm l; sepals 12–14, the outer pair opposite, suborbicular and connate, the inner imbricate, to 15 mm l and 18 mm w, the inner becoming oblong with narrowed base; petals 8, obovate, 3–4 cm l.

♂ flowers: unknown.

♀ flowers: staminodia 4–5 mm l, numerous, free, linear, sterile, 4–6-serial; ovary 16-celled, ovules numerous, 2-ranked, sessile, oblong; styles 16, 2–4 mm l, free, radiating from a crateriform beak 1–3 mm l; stigmas obovate-oblong, ca. 2 mm l, subbasally attached, articulate. Fruit 3–4 cm l, oval-oblong; seed oblong-ovoid ca. 3 mm l.

Distribution: Suriname.

Tafelberg: small branched tree to 5 m h, petals white, fragile, crimped and erose along the margin, frequent, edge of Savanna V, Aug. 16, 1944. *Bassett Maguire 24396* ♀ (holotype NY); Savanna II, *Maguire 24245* ♀, *24738* ♀. Wilhelmina Gebergte: Juliana Top, 1000–1230 m alt. Aug. 18, 1963. *Irwin et al. 54879* ♀.

3. **Clusia sessilis** Klotzsch ex Engl. Sect. Anandrogyne Pl. & Tr.
Clusia cerroana Steyermark, Fieldiana, Bot. 28: 386. 1952.

Tree 3–20 m h, latex clear, moderate; branchlets 5–12 mm diam, terete, internodes commonly 2–5 cm l; leaves sessile; blades subcoriaceous, broadly to narrowly oblanceolate, commonly 10–25 cm l, 5–14 cm w, the apex broadly rounded, narrowed to the clasping base; midrib depressed above, prominent and raised beneath, extending to the apex; primary veins 2–3 mm apart, rising at a 25°–40° angle, collected in a peripheral vein 1–4 mm from the margin. Inflorescence terminal, commonly 3–5-flowered; peduncles stout, to 3 cm l, sometimes lacking; primary bracts sometimes foliar, secondary bracts broadly rounded, wider than long; bracteoles lacking; flowers fragrant.

♂ flowers: sepals 4, decussate, broadly semiorbicular, 6–10 mm l, 10–15 mm w, the inner pair larger. Petals 5(6), oblong to oval-oblong, 15–22 mm l, 8–16 mm w, yellowish-green. Receptacle shallowly cupulate. Stamens linear, numerous, ± 100, free, the outer filaments borne on a low corona, filaments reddish-brown, 3–6 mm l, compressed, 0.4–0.6 mm broad; anthers contrastingly cream-white, 5–6 mm l, laterally dehiscing for their entire length; pollen 3-colporate, sphaeroid-deltoid, essentially isolateral, in equatorial view 32.5–34.5 μ, sporoderm relatively thin, 2–2.5 μ thick, not thickened toward pores; crystals present.

♀ flowers: sepals 4, decussate, broadly semiorbicular, 6–8 mm h, 8–12 mm w. Petals 5(6), oblong to oval-oblong, 14–18 mm l, 6–10 mm w, yellowish-green. Staminodia lacking. Ovary flask-shaped, 5 (4–6)-celled; stylar processes stout, cornute; stigmas terminal, more or less peltate, obtusely deltoid; ovules several, 1–2-ranked, ascending, aril delicate, becoming hyaline. Fruit subsucculent, the body to 2 cm l, the cornute styles to 1 cm l; seed oblong, to 5 mm l.

Distribution: chiefly of the Roraima sandstone regions of Guayana, where it is common.

In Suriname known by two collections, both from Juliana Top, Wilhelmina Gebergte, and both staminate: very common on exposed spots all over summit between 1000 and 1200 m, terrestrial or epiphytic in low trees. Aug. 8, 1963. *J. P. Schulz 10302* ♂; tree 10 m high, densely branched to the ground, on upper slopes and summit of Juliana Top, at 1000–1230 m alt. Aug. 8, 1963. *Irwin et al. 54862* ♂.

The flowers of Wilhelmina specimens are somewhat larger than the average, and the color of the petals is noted as "white" and "dirty white". It is possible that the two collections cited above represent a geographic variant. Dr Schulz notes that the plant may be an "epiphyte in low trees". Otherwise there is no record of the species other than terrestrial.

4. **Clusia melchiori** Gleason, Bull. Torrey Club 58: 403–404. 1931. Sect. Eucriuva Engl.

Cl. flaviflora Eyma, Med. B. M. Univ. Utrecht 4: 130. 1932, not Engler in Engl. Bot. Jahrb. 58, Beibl. 130. 1923.

Small or medium tree to 18 m h; younger branchlets stout, angled, soon becoming subterete, latex moderate, clear, oxidizing reddish-brown. Leaves: petioles stout, 5–18 mm l, 5–16 mm w; lamina oblong-obovate to broadly obovate, rounded at the apex, often cuneately narrowed toward the base, (5) 10–20 cm l and (4) 8–15 cm w, coriaceous; midrib prominent and canaliculate above, continuing but diminishing toward the apex, prominent beneath, primary veins equally prominulous on both sides, 2–4 mm apart, making a 45° angle with the midrib, joining a peripheral nerve ± 1–4 mm from the margin. Inflorescence terminal, ternately or quadrately decompound, often botryoid, to 12 cm l, many-flowered; peduncle to 4 cm l, the stout axis and branches sharply angled, the ultimate very short, 0.5–2.0 mm l, bracts and bracteoles ovate to deltoid-acute, 2–5 mm l; flowers subsessile or the pedicel 1–2 mm l, flowers, especially those of the male plants, very fragrant, petals 4, pale greenish-yellow.

♂ flowers: bracteoles 4, decussate, subcarinate, ovate, acutish, the upper pair somewhat rounded, 1.5–2.0 mm l; sepals 4, decussate, the outer pair broadly ovate ca. 2.5 mm l, the inner orbicular-ovate, ca. 4 mm l, subhyaline, the margin broadly scarious; petals 4, elliptic-oblong, 3.5–4.0 mm w, 5.0–6.0 mm l, subcarnose toward the base; stamens normally 16–20, filaments free, 2.5–3.5 mm l, the outer shorter, radially somewhat compressed, ca. 0.4 mm w; anthers 1.2–1.5 mm l, oblong, completely laterally dehiscing, connective prominent, not productate; pollen grains 3-colporate, in equatorial view deltoid, essentially isolateral, 25–30 μ diam, intermixed with numerous spherical, mace-like crystals 10–20 μ diam; abortive pistil lacking.

♀ flowers: bracteoles 6–10, closely imbricated, decussate, subcarinate, broadly ovate-suborbicular, 2–3 mm l, sepals 4, hardly separable from bracteoles, scarious-margined; petals 4, oblong-oboplate, 5–6 mm l, 3–4 mm w, subcarnose, greenish-yellow; staminodia vacking; ovary 4-celled, each cell with a single ovule, seldom 2; capsule fleshy, ovoid-globose, 6–15 mm l, abruptly narrowed to a short stylar portion surmounted by 4 ovoid connivent stigmas, 0.8–1.0 mm l, the normally solitary seed oblong, 4–10 mm l, with a separable hyaline testa.

Distribution: sandstone region of the Guayana Highland and on Tafelberg, and proximal mountain tops in Suriname.

Suriname: Emma Keten, top II, at 700 m alt. (*B.W. 5645*, young fr., March 1932) (U); Hendriktop, at 1080 m alt. (B.W. n. *5665*) (U); Tafelberg, East Ridge at 760 m alt., Sept. 1944. *Maguire 24585* ♀, *24585a* ♂; Tafelberg, Savanna VIII, at 564 m alt., Sept. 1944. *Maguire 24641* ♀; Wilhelmina Mts., Juliana Top at 1050 m alt., Aug. 4, 1963. *Schulz 10296* ♀, *10303* ♂; *Irwin et al. 54864* ♂.

Clusia melchiori does indeed belong to a "coherent" group of species of northern South America and the West Indies, as indicated by Eyma (Med. B. M. Univ. Utrecht 4: 14. 1932) in his consideration of the Suriname plant under the name *Cl. flaviflora*. Most students of *Clusia* have recognized these relationships, under which probably fall *Cl. havetioides* (Griseb.) Pl. & Tr. and *Cl. krugiana* Urb., in the West Indies; *Cl. melchiori* Gleason, *Cl. cardonae* Maguire, and *Cl. opaca* Maguire in Guayana and Suriname; *Cl. pseudo-havetia* Pl. & Tr., *Cl. trochiformis* Vesque, *Cl. poeppigiana* Engl., *Cl. veneralensis* Cuatrecasas, and others of the Andes.

These species appear to belong to the large and complex *Section Anandrogyne* Pl. & Tr., and may well comprise a distinct subsection within it. Since the delimitation of species and consequent nomenclature of them is not at this time understood, the epithet *melchiori* is here best employed to cover the plants so defined for Suriname and contiguous British Guiana and Venezuela.

5. **Clusia pana-panari** (Aubl.) Choisy in D. C. Prodr. 1: 559. 1842. Sect. Pseudo-quapoia Engl.

Quapoya Pana-panari Aublet, Hist. Pl. Guiane fr. 2¹: 900. 1775.
Renggeria guyanensis Splitg. in Tijdschr. Nat. Gesch. 9: 104. 1842.
Quapoya surinamensis Miquel, Stirp. Sur. sch. p. 92. 1851.
Clusia colorans Klotzsch ex Engl. Fl. Bras. 12¹: 426. 1888.
Clusia microphylla Klotzsch ex Engl. Fl. Bras. 12¹: 426. 1888.

Shrub, small or medium tree, often epiphytic; latex moderate clear, whitish or milky. Leaves: petioles slender 5–15 mm l; lamina subcoriaceous, obovate to oblanceolate, commonly 8–12 cm l and 3–5 cm w, less often as small as 3 cm l and 1.5 cm w; rounded or obtusely pointed at the apex, gradually and acutely narrowed to the base; midrib somewhat prominent beneath, prominulous above, diminishing toward the apex, primary veins prominulous beneath, inconspicuous or non-evident above, forming a 40°–45° angle with the midrib, canals often conspicuous above, forming a 50°–60° angle with the midrib. Inflorescences terminal, ternate or ternately decompound, often compact, usually 3–5 (9)-flowered, their branches angled, commonly 2–3 cm l, essentially sessile, pedicels 1–6 mm long; bracts ca. 1 mm l, rounded, bracteoles 4, decussate, sepals 5, imbricate, 3.0–4.5 mm l, broad lyrounded, conspicuously brown-scarious-margined; petals 5, pale greenish-white, yellowish or greenish-orange, reddish maculate within, 5–7 mm l.

♂ flowers: stamens usually 15–25, rarely as few as 5, free, forming a subglobose central compacted mass; filaments stout, angled by compression, ca. 1.5 mm l; anthers distally lateral, opening by 2 terminal pores, the connective diameter broader; pollen grains 3-colporate, sphaeroidal, 24.5–28 μ diam; sporoderm thickened at pores, crystals few, 7.5–19.5 μ diam. Flowers containing a rudimentary pistal usually provided with 8–10 stamens.

♀ flowers: staminodia 5, somewhat broader than stamens of the male flower; ovary 5-celled, each cell with 3–6 ovules, sessile, aril basal, copious, fimbriate, yellow; stigmas 5, deltoid-rhombic, sharply acute, connivent, 2–3 mm l, hispidulous. Fruit turbinate-obovate, 8–14 mm l, at maturity most often strongly transversely rugose when dry because of the transverse cartilaginous thickening of the endocarp walls; seed oblong 3–4 mm l, aril persistent.

Distribution: the region of Coastal Guiana, Venezuela to Brazilian Amazonas and Maranhão.

Commonly distributed in Suriname as a shrub or small tree in open area, especially along water courses, and in forest areas as an epiphyte.

The species is somewhat variable in size of leaf, leading to the two names, *Cl. colorans* and *Cl. microphylla*. The taxonomy is not entirely clear because of the apparent failure of some specimens with large fruit to develop the characteristically rugose form, in which no perceptible cartilaginous thickening occurs. In this condition the stigmas may be smaller and less connivent. There is considerable variation in the number of stamens, in some plants of Amapá there being as few as 5.

6. **Clusia scorbiculata** Benoist, Bull. Hist. Nat. Paris 30: 511. 1924. Sect. Polythecandra Pl. & Tr.

Distribution: Guiana; British Guiana to Amapá, Brazil.

The few specimens by which this Guianan species is known indicate that it is an epiphytic strangler. Its near relative in southeastern Brazil, *Cl. fluminensis*, is more often a bushy tree – and is commonly planted in this form as an ornamental. Other close congeners, notably *Cl. schomburgkiana* and *Cl. modesta* of the Guayana Highland region of Venezuela and adjacent British Guiana, Brazil and Colombia, are bushy trees to 15 m in height.

To this time, apparently no wholly staminate material has been collected. All material examined seems to be hermaphroditic or partially so.

Brazil: "Epifita em arvores, Igarapé Pontanarri, Rio Oiapoque", Feb. 14, 1950. *Fróes 26017.*

British Guiana: Parasitic shrub, Onoro Creek, Essequibo River, Dec. 15–24, 1937. *A. C. Smith 2736.*

Suriname: Brownsberg, Nov. 6, 1915. *B.W. 759;* epiphyte, Nassau gebergte, Feb. 23, 1949. *Lanjouw & Lindeman 2264;* epiphyte, Capoerica Ridge, Perica, Jan. 21, 1954, *Lindeman 5338;* epiphyte, latex abundant, yellowish, oxidizing blood-red, Jodensavanne–Mapane Creek, Suriname River, Dec. 21, 1954, *Lindeman 6943.*

7. **Clusia purpurea** (Splitg.) Engler, Fl. Bras. 12^1: 416, t. 86, f. 2. 1888. Sect. Phloianthera Pl. & Tr.

Arrueda purpurea Splitgerber in Tijdschr. Nat. Gesch. IX, p. 102. 1842. *? Clusia leprantha* Mart. Nov. Gen. et Sp. 3: 165. 1829.

Distribution: Suriname (and probably British Guiana) south to Maranhão, Brazil, the Amazon Basin to Loreto, Peru, and Amazonas, Colombia and Amazonas, Venezuela.

Suriname: Surinam, Nov. 1846. *Hostmann (Kappler) 1704;* Gran Dam, Saramacca River, Oct. 11, 1944. *Maguire 24934* ♀ (fr.); Moengo, Dec. 24, 1954. *Maguire 38976* ♂; Paramaribo, Nov. 1, 1955. *Lindeman 6639* (sterile); Tigri-hedde, Coppename River, Nov. 17, 1954. *Lindeman 442;* Lucie River, July 2, 1964. *Maguire et al. 54070* ♀ (fr.).

In all probability the Guianan populations are conspecific with those of the upper Amazon Basin. At least at this time I cannot recognize any distinction. If it is to be demonstrated that a single species in fact obtains, then the name *Clusia leprantha* will have to take precedence.

Pistillate flowering material was not available to Eyma (Fl. Surinam 3: 96. 1934). At this much later date female flowers are still lacking to me. Two inadequate ♀ specimens (Froés 1750, 29460), both from the eastern Amazon Basin, may shed some light as to the morphology of ♀ flowers. The androecium in *1750* has numerous, 7–8-serial, free, massive, prismatic stamens, and *29460* is similar but with 4–5-series of evidently functional stamens. Contrastively, the large amount of ♂ material uniformly possesses the typical conic synandrium. Alternatively, the two cited Brazilian specimens may represent yet another species. Resolution of the problem must await more observation in the field, and better and more extensive material. All collections of fruiting material seen by me are without a trace of androecium.

8. **Clusia fockeana** Miquel, Tijdschr. Nat. Gesch. 10: 82. 1843. Sect. Androstylium (Miq.) Engl.

Cl. stahelii Maguire. Bull. Torrey Club 75: 424. 1948.

Distribution: Guiana, from British Guiana to Pará, Brazil.

Cl. fockeana is a common shrub or small tree of savannas or open sites in the Guianas. It is sometimes epiphytic. There appear to be no immediate relatives of this species, which is well marked, readily recognized, and which belongs to the small *Section Androstylium.*

9. **Clusia minor** Linnaeus, Sp. Pl. Ed. 1: 510. 1753. Sect. "Minor".

? *Cl. parvicapsula* Vesque, Epharm. 3: 10. pl. 34. 1892.
? *Cl. cartilaginosa* Vesque, in D.C. Monogr. Gutt. 8: 97. 1893.
? *Cl. utilis* Blake, Contr. U.S. Nat. Herb. 24: 14. 1922.

Distribution: West Indies and northeastern South America, probably also the northern Andes and Central America.

Clusia minor L., the second of the original Linnaean species of the genus (see HOWARD, Jour. Arn. Arb. **43**: 394. 1962), has since the early history of the genus been a poorly understood and interpreted species. Yet, it is widespread, strongly marked, and a not unusually variable species. Notwithstanding, the three binomials, viz., *Cl. cartilaginosa* Vesque, *Cl. parvicapsula* Vesque, and *Cl. utilis* Blake, have been derived from *Cl. minor*, or at most represent weak segregates of it.

Fruits vary somewhat in size, but are all surmounted by the characteristic upturned radiate stigmas. Leaves also vary somewhat in size but retain fundamental form, venation and prominence of latex canals.

Perhaps the bisexual character of the flowers, unusual in the genus, except in the *Sect. Polytheca*, has led to some confusion and certainly to the exclusion of the species or derivatives from any sectional classification. In another place I shall address this problem. Elsewhere in *Clusia* an element of functional bisexualism obtains, notably in *Sect. Polytheca*, where in essentially pistillate trees flowers normally form anthers with evidently functional pollen.

10. **Clusia nemorosa** G. F. W. Meyer, Primitiae Fl. Essequeboensis p. 203. 1818. Sect. Clusia.

Distribution: Venezuela, Guiana and Brazil, extending south to Rio de Janeiro.

Commonly a shrub or small tree characteristic of savannas or open sites. *Cl. nemorosa* is the only member of the *Sect. Clusia* with the ovary developing as few as 5 cells. Characteristically, members of the section are 10–18-carpellate.

11. **Clusia grandiflora** Splitgerber, Tijdschr. v. Nat. Gesch. 9: 101. 1842. Sect. Clusia.

Distribution: Guiana in the broad sense, extending from Venezuela to Pará, Brazil.

Clusia grandiflora is perhaps the finest of the many species of the very large and generally ornamental genus *Clusia*. Its range seems to be restricted to the Guianas, and is therefore not wholly coextensive with that of the complex *Section Clusia*, the members of which are to be found in the Antilles and in northeastern South America, inclusive of the Amazon Basin. *Cl. grandiflora* is easily distinguished from its immediate congeners by its large flowers, the showiest of the genus, its large depressed globose fruit, and its stout, conspicuously angled younger internodes. The bush or tree form is cultivated in Venezuela and Brazil.

12. **Clusia platystigma** Eyma, Polygon., Guttif., Lecyth. p. 29, fig. 4. 1932. Sect. Clusia.

Distribution: Suriname to Pará, Brazil.

In flowering pistillate and fruiting specimens, *Cl. platystigma* is easily separable from other euclusioids of Suriname and Guiana because of the flat, non-raised stigmas and subsulcate fruit. *Cl. platystigma*, a small tree or an epiphyte, is immediately related to yet undescribed species of the upper Río Guainía and upper Río Atabapo in Amazonas, Venezuela.

Suriname (in addition to specimens cited by Eyma): Zanderij I, Apr. 28, 1945. *Stahel 295;* Moengo, Nov. 22, 1949. *Lanjouw & Lindeman 406;* Jodensavanne–Mapane Kreek area, July 10, 1953. *Lindeman 4218.*

Brazil: Serra do Navío, Amapá, Nov. 8, 1954. *Cowan 38147.*

13. **Clusia robusta** Eyma, Polygon., Guttif., Lecyth. p. 29, fig. 4. 1932. Sect. Clusia.

Distribution: Known presently only from central Suriname.

Suriname: Tree 10 m h, Hendriktop at 1080 m alt., Mar. 13, 1922. *B. W. 5728* ♂ (holotype U); shrub or small tree to 8 m h, frequent, borders of Savanna VIII, Tafelberg, Aug. 29, 1944. *Maguire 24569* ♂, *24570* ♀.

Clusia robusta is apparently known only from the cited localities. It is readily recognized in staminate flower by the muticous anthers, and by the deeply sulcate fruit. In this latter respect it resembles undescribed relatives of *Cl. platystigma*, which have been found in Amazonian Venezuela. The several related species are all trees.

14. **Clusia palmicida** L. C. Rich. apud Pl. & Tr., in Ann. Sc. Nat. ser. 4, 13: 326. 1860. Sect. Clusia.

Distribution: Guiana in the broad sense, extending from Venezuela to Pará, Brazil.

Probably most often an epiphyte, its habit indicated by its name. *Cl. palmicida* and its near relatives are not clearly understood. Little is added to the knowledge of its biology in this paper. A thorough examination of the *Sect. Clusia* is needed before acceptable interpretation can be offered. Indeed, this holds true for the entire section.

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THE HIBERNATION OF THE OAK MILDEW

L. C. P. KERLING[1]

(Phytopathologisch Laboratorium "Willie Commelin Scholten", Baarn)

(received October 19th, 1965)

The oak mildew invaded Western Europa in the years 1908 and 1909. Since then this parasite, *Microsphaera alphitoides* Griff. & Maubl. (syn. *M. quercina* (Schw.) Burr.) has occurred regularly in the Netherlands on oak seedlings and oak coppice, mainly *Quercus pedunculata* Ehr. (syn. *Q. robur* L.). After the appearance of the fungus its identity and also its mode of hibernation has been amply discussed. Perithecia with ascospores were discovered by Arnaud and Foëx (1912) in France. In the Netherlands perithecia were only occasionally observed, as their occurrence seems to depend on weather conditions during the summer months (Hartsuyker, 1939). Besides ascospores, if present, chlamydospores on old infected leaves described by Ferraris (1909) might be a source of infection of young leaves in spring (Petri, 1923). However, these observations were not confirmed by other investigators.

Neger (1911), Peglion (1911), and somewhat later also Van Poeteren (1912) observed hibernation of the mildew in infested buds from which malformed shoots developed in spring, stem and leaves being covered with mycelium and conidia. Woodward *et al.* (1929) described the way the mildew spreads: conidia from these shoots infect young healthy leaves in the neighbourhood, on which circular colonies develop. The growth of these white patches stops rather soon, probably owing to thickening of the cuticle of the ageing leaves. As has been noted by Ditu *et al.* (1964) leaves are severely attacked up to the age of 20 days. A second outbreak may occur on the newly developed Lammas shoots. Van Poeteren (1918) gave a clear description of the two periods of spread.

According to Woodward *et al.* young buds developing in the axils of mildewed leaves may contract infection when the scales are still young, soft, and loosely applied. Under such conditions the mildew "enters the bud where the mycelium may become established on the softer tissues of the scales and subsequently between the leaf initials. As the buds grow older the scales become tough, more tightly applied, and then afford complete protection from infestation". In their experiments with hundreds of heavily infected plants the authors found only a few trees to carry infected shoots in the following spring. The chance a bud will become infected seems to be extremely low.

According to Van Poeteren (1912 and 1918) hibernation of the mycelium will take place between the scales of a small number of buds. GÄUMANN (1951) is of another opinion: mycelium may hibernate on the bud scales from where it may infect the underlying leaf initials at the time of budbreak in spring.

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[1] In cooperation with E. C. J. Ott.

None of the investigators describing perennation in or on buds refer to their site at the stems or to the time at which they may become infected.

The purpose of our study was to make out at which time of the season which buds will have a chance to become infected.

The spread of the mildew was observed on oak coppice grown on sandy soils in the centre of the Netherlands during two seasons from spring unto autumn of 1961 and 1962. Bud development was studied mainly in 1965. Experiments were carried out with a group of 100 oaks planted in the garden of the laboratory. All oaks belonged to *Quercus pedunculata.* No fungicides were applied.

OBSERVATION ON MILDEW INFECTIONS

Every year, earlier or later in April, depending on weather conditions, bud break occurs. The spring shoots usually develop from the apical bud or the highest axillary ones of the Lammas shoots formed in the year before. If a Lammas shoot is lost, which is frequently the case, the new shoots develop from the axillary buds of the one year old spring shoots. The axes of the buds stretch slowly, scales, ligulae and leaflets expand gradually, and though individual trees develop their shoots far from simultaneously, the new shoots are full grown in the beginning of June.

In 1961 oak coppice was regularly observed over a vast area. In the first week of May about 75 heavily contaminated shoots were found on low shaded branches, as a rule not more than one per tree. They had originated from buds present on shoots formed in spring 1960 (Fig. 1a). The Lammas shoots of that year had disappeared, they had probably been heavily infected by mildew. It is known that such shoots do not survive the winter. Also Woodward *et al.* found contaminated shoots "mostly at the base of the previous year's shoots, the upper portion of which had been killed by a severe attack of mildew".

The basal parts of the stems and the leaves of the contaminated shoots were covered with mycelium and conidia. Specially the basal leaves were partly or totally malformed. Some shoots were only unilaterally infected and misshapen.

As soon as these shoots had expanded infection of the young surrounding leaves occurred, at first within a radius of about half a meter, later mildewed leaves were found in a bigger area around the source of infection. Colonies became visible when the leaves had reached a length of about one cm. They enlarged until the leaves were dark green and mature. Then further spread of mildew was not observed.

After mid-June the apical bud and sometimes also three to five axillary buds of the spring shoots suddenly started elongating, which

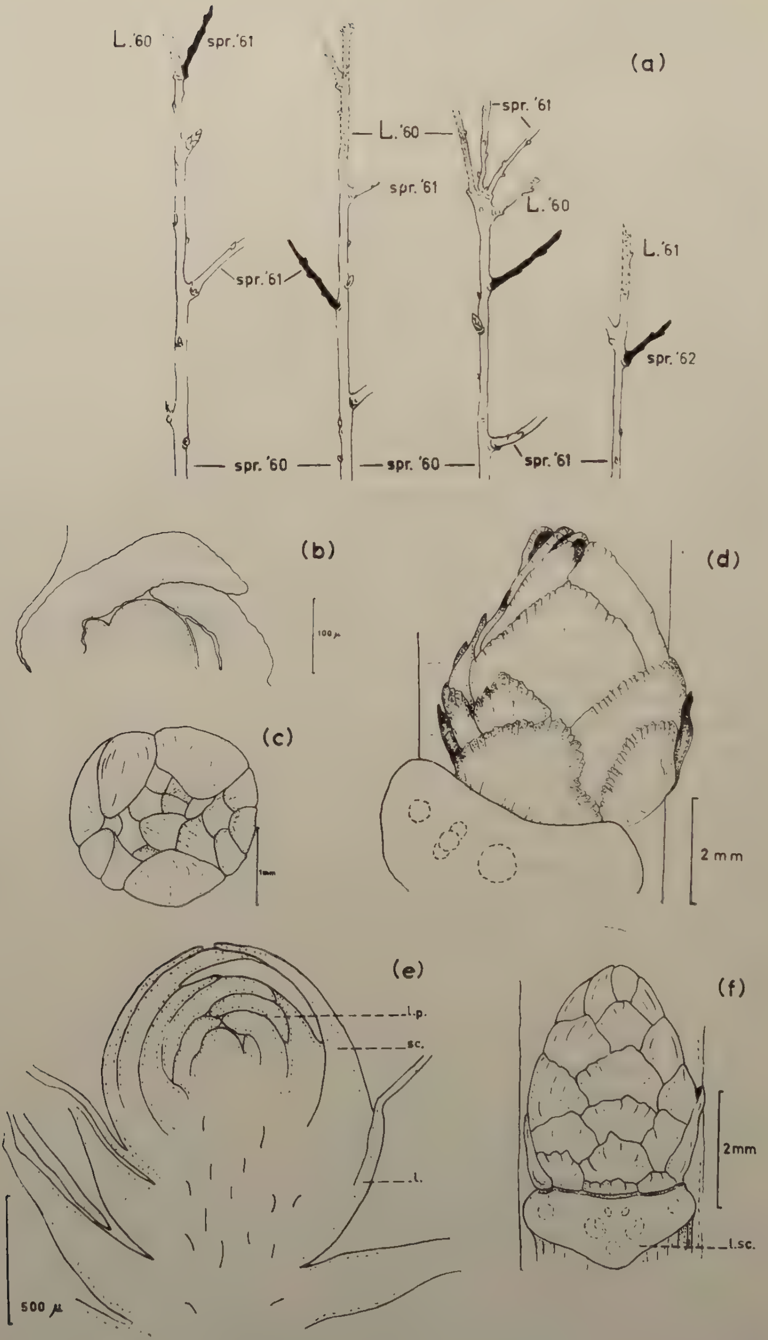
(a)
L.'60
spr.'61
L.'60
spr.'61
spr.'61
spr.'61
L.'60
L.'61
spr.'62
spr.'60
spr.'60
spr.'61
(b)
100 μ
(c)
1mm
(d)
2 mm
(e)
l.p.
sc.
l.
500 μ
(f)
2mm
l.sc.

Fig. 1.

resulted in the formation of the Lammas shoots. They could reach a length of 30 to 40 cm in about a month time, carrying a range of growing leaflets at their tips. All leaves and also the stems became readily covered with mildew. Conidia present on the leaves of the spring shoots were probably the source of contamination, for at that time the mildewed and malformed spring shoots had already shed their leaves.

The younger the leaves of the Lammas shoots were attacked the more they became malformed. At the end of August the tips with the apical buds of heavily mildewed shoots started to die off. The infection potential seemed to have reached its maximum.

BUD DEVELOPMENT AND POSSIBILITY OF INFECTION

More than half of the 75 heavily contaminated shoots found in spring 1961, were situated at the distal third part of the spring shoots formed in 1960, the others were situated lower. From this observation and the disappearance of the Lammas shoots it became evident that hibernation takes mainly place in the highest buds of the spring shoots and not in those of the Lammas shoots.

The question was raised at which stage the buds of the spring shoots might become infected.

Healthy, overwintered buds ready to break in spring, are somewhat conical with a length of about 2 to 5 mm. They may contain about 30 to 50 brown scales, from which the outer, shorter ones, are oldest and darkest. The younger ones partly overlap each other, while the youngest inner ones are tightly folded over the leaf initials in such a way that their margins alternate with the bases of the scales situated at the opposite side of the buds. Hairs are inserted in the margins of the about 30 to 50 scales. There may be 8 to 10 leaf initials, each with a pair of ligulae and a meristematic tissue at its base: the vegetation point of the future axillary bud. During bud break, stem

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Fig. 1. a. Scheme of 4 spring shoots observed between May 16 and 19.
L: Lammas shoots.
spr.: spring shoots.
dotted: Lammas shoots dead or disappeared.
black: infected spring shoots.
b. Young flat bud developed in the axil of a leaflet of the apical bud of a spring shoot (June 29).
c. Closed spherical bud in the axil of the third leaf of a spring shoot, covered by scales and seen from above (June 26).
d. Elongated axillary bud situated on a spring shoot under two Lammas shoots (July 23).
e. Longitudinal section of a conical axillary bud of a spring shoot. The lower bracts and stipulae have been cut away; others loosened by the treatment (July 1).
sc.: scales.
l.: ligulae.
lp.: leaf primordia.
f. Conical bud on a spring shoot, situated under a Lammas shoot (October 4).
l. sc.: leaf scar.

elongation and leaf expansion, these axillary growing points split off primordia, first the initials of the future outer scales, which fully enclose the vegetation point. Buds with one to four scale initials are still flat. They are found in the axils of leaflets that have just become macroscopically visible (Fig. 1b). The younger scale and leaf initials develop in succession. In turn they are first applied to the vegetation point and then pressed towards the outside of the bud by the initial that develops next. During this process of growth the shape of the buds becomes more and more spherical. By the end of May, when the shoots are fully developed and the leaves initially present in the overwintered buds have expanded, the axillary buds of these leaves show a scala of developmental stages: the flat upper ones with a width of about ½ mm, still consisting in a vegetation point surrounded by only a few soft green scales, the basal ones with a diameter of about one mm, covered by 5 to 8 scales from which the margins begin to discolour. All buds are tightly closed, though the outer scales of the oldest ones are applied laterally only (Fig. 1c). In June all buds are covered by brown scales and they may contain 10 or more initials. The tips of the shoots show a number of ligulae, leaflets and initials from which the green tips are visible. Further development stops, however.

The question arose, whether the buds of the young spring shoots can become infected. According to Woodward *et al.* the mildew can only establish itself on very young buds with soft green scales. Only shortly after bud break are the buds in the axils of the basal leaves still in that condition, but at that time one scarcely finds mildewed shoots producing conidia. Therefore these buds may escape infection. This might also be the case with the topmost buds. Though they develop later, at the time mildewed shoots have developed, they remain protected by ligulae and growing leaflets for a long time. The scales of all buds darken rapidly after they have become exposed. The condition for contamination of soft green buds seems but seldom to be fulfilled. For that reason Woodward *et al.* consider the rapidity with which the bud scales harden to be the cause of the low percentage of bud infection. Moreover, the infection potential remains usually low at that time of the season. Still, contamination in this early stage of the epidemic should not be excluded, since development of the shoots of different trees is not simultaneous. It may occur that conidia from a full-grown infected shoot will contaminate young buds of a neighbouring tree that is less advanced in shoot development.

That mycelium might grow between the scales and the leaflets of a contaminated bud as Woodward *et al.* suggest, seems, however, unlikely in this stage. These parts cover each other and the vegetation point tightly from the very first stage of bud development. Microscopic examination never revealed mycelium of mildew at the inner side of these buds.

After the second decade of June the condition of nearly all buds changes rather suddenly. Besides the spectacular development of longer or shorter Lammas shoots from the apical and the highest buds, also the buds situated under these rapidly growing shoots start elongating, but at a much lower rate. Some may still produce new shoots as late as the end of July or in August (Fig. 1d), but the majority of the buds, however, stops growing when they have reached a length of 2 to 5 mm. Their shape becomes conical instead of spherical, which is due to the stretching of the axes, following which the outer scales become more loosely applied to each other, hardly overlapping each other. Only the inner ones do remain tightly applied to the leaf primordia (Fig. 1e and f).

In this condition the buds overwinter, and it is in these buds that the fungus might hibernate. They are exposed to clouds of conidia from the severely infected Lammas shoots on top of them.

That they may become infected was observed in August 1961, when such a bud started new growth. It gave rise to a heavily infected shoot, similar to those that develop in spring. If it had remained dormant it would probably have shown the infection after winter.

Microscopical examination of those conical buds overgrown with mildew revealed mycelium on the green or slightly discoloured superficial parts of the scales, entangled with the marginal hairs. Neither on the innerside nor on the covered parts of the scales was mycelium found.

EXPERIMENTS

Only a few experiments out of many were successful. Branches were cut off just above inoculated buds in order to study a possible infection of the developing shoots, but no infection occurred. Only bringing conidia between the loosely applied scales and leaflets of the apical buds of spring shoots did result in spread of the mildew on stem and leaves of the developing Lammas shoots. If a bud had been inoculated laterally, the leaves of the Lammas shoot also showed a one sided infection. The disease symptoms did not differ from those of infected shoots in early spring.

In another experiment a young Lammas shoot with a length of 5 cm and leaflets of ½ to 1 cm on a healthy tree was inoculated in July 1961. It soon became covered with mycelium. During the following winter it died off, but in spring 1962 an infected shoot developed from a bud at the tip of the spring shoot of 1961 (Fig. 1a). Probably conidia applied to the Lammas shoot or produced on the Lammas shoot itself had contaminated this bud, in which or upon which the fungus hibernated.

CONCLUSION AND SUMMARY

It was observed that infected spring shoots usually develop from buds situated at the highest parts of spring shoots formed in the previous year, the Lammas shoots of which had died off during winter. Therefore the development of the buds on spring shoots was studied in relation to the possibility of contamination and infection with mildew. Initially the young buds are flat, their vegetation point being surrounded by a few scales. Later, when more scales are developed, they become spherical. During the first period of the mildew epidemic infection of these buds is unlikely, since it seems impossible for mycelium to enter these tightly closed buds. Even overgrowing can hardly be expected, because the highest buds at least will remain covered by ligulae and leaflets for a long time during shoot development. Moreover, the scales harden quickly and infection potential is still low.

Contamination of the buds of the spring shoots probably occurs during the second period of the mildew activity from July until autumn, when there is an abundant production of conidia in the Lammas shoots. At that time the highest buds of the spring shoots that did not produce Lammas shoots have become conical, following a process of elongation which stops when the buds have reached a length of 2 to 5 mm. The outer scales overlap each other only partly and they become less tightly applied to the core of the bud containing the inner scales and the leaflets. Hyphae could be observed, covering the superficial, only slightly discoloured parts of the scales.

Considering the heavy spore loads present around the infected Lammas shoots, the number of outwardly contaminated buds must be high. Still hibernation occurs relatively seldom. Probably the dark brown scales of most buds are unsuitable for infection. They are mostly too tightly applied to each other to allow the fungus to reach the underlying soft green tissue. It is not impossible that mycelium settles itself on the hairs or on green parts of some bud scales, where it may remain dormant. At the time of bud break it might infect the underlying initials, as it has been assumed by Gäumann.

This way of hibernation is, however, unlikely, since the buds during their transition from spherical to conical do not show superficial green parts, and the hairs die off fairly soon. It is more likely that mycelium entangled in the hairs of bracts or even conidia might penetrate incidentally between the outer, somewhat loosened scales of some buds, where the fungus can settle itself on underlying soft tissue. Here it may hibernate, as has been suggested by Van Poeteren. It can thus be explained that infected shoots develop mainly from the highest buds of the spring shoots situated under the Lammas shoots, since it is these ones that show the greatest elongation at the end of June. In this way a unilateral infection of spring shoots can be accounted for as well as the fact that the stem and the basal leaves often show the heaviest infection: these parts are the first to become infected by mycelium present between the outer, loosened scales.

ACKNOWLEDGEMENT

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BISTELLA ADANS. VERSUS *VAHLIA* THUNB. (VAHLIACEAE)

A. A. BULLOCK

(The Herbarium, Royal Botanic Gardens, Kew, England)

(received October 30th, 1965)

The somewhat peculiar genus *Vahlia* Thunb. (1782) was formerly regarded as an anomalous member of the *Saxifragaceae*, but in 1959 it was segregated as the monotypic family *Vahliaceae* by DANDY (in HUTCHINSON, Fam. Fl. Pl. ed. 2, 1: 461). The genus includes about three species, all of them highly variable in stature, flower size, and indumentum; this has resulted in the description of more than twenty "species", whose names now appear in synonymy. This note, however, is chiefly concerned with the generic name, since it appears that *Vahlia* Thunb. is not correct under the Code and must be replaced by *Bistella* Adans. (1763). In the synonymy under the new combinations, all the relevant names so far traced are included, but it may well be that an experimental approach to the problem of specific and infraspecific limits and the taxonomic value of the characters hitherto relied upon for differentiation would result in considerable changes.

Bistella Adans. (1763) was cited in the form "*Bistella* Lippi 243 – *Ascyroides* Lippi" and the name than fell into abeyance until it was resuscitated by Delile in 1826. He described plants collected by Cailliaud, and identified a number of them with those of Lippi. In particular, he identified Lippi 243 (and 244) with the Cailliaud plant which he named "*Bistella geminiflora* Delil. (Descript. des plantes découv. par M. Cailliaud, pl. II. fig. 4). – *Ascyroides* Lippi (Manusc. nos. 243 et 244)." It must be emphasized that the taxonomic identification of "*Bistella* Del." with *Vahlia* Thunb. has never been questioned, but the identity of Adanson's *Bistella* with *Bistella geminiflora* Del. has been overlooked; this species, as represented by Lippi's plant, is the type of the generic name *Bistella* Adans.

The resuscitation of Adanson's generic name does not affect the family name *Vahliaceae* since *Vahlia* Thunb. is a legitimate generic name although now relegated to synonymy. Conservation of *Vahlia* is not proposed, the genus being of little interest to any except taxonomic botanists.

The genus ranges from south-western Africa to the Orient, Pakistan and India and it occurs in arid and semi-arid areas.

Relevant literature citations and necessary new combinations are as follows:

Bistella Adans. Fam. Pl. 2: 226 (1763); Del. Cent. Pl. Afr. 7 (1826), & Voy. Méroé 2: 97, *t. 2, f.2* (1826). Typus: *B. geminiflora* Del. [syn. tax. *B. digyna* (Retz.) Bullock].

Russelia Linn. f. Suppl. 24 (1781), non N. J. Jacq. (1760). Typus: *R. capensis* Linn. f. [*Bistella capensis* (Linn. f.) Bullock].

Vahlia Thunb. Nov. Gen. Pl. 2: 36 (1782); Hooker f. in Bentham & Hooker f. Gen. Pl. 1: 637 (1865); Engler in Engler & Prantl, Nat. Pflanzenf. III. 2A: 65 (1890) et ed. 2, 18A: 166 (1930). Typus: *V. capensis* (Linn. f.) Thunb. [*Bistella capensis* (Linn. f.) Bullock].

Bistella dichotoma (Murray) Bullock, comb. nov.

Heuchera dichotoma Murray, Comm. Gotting. 64, *t. 1* (1772).

Oldenlandia pentandra Retz. Obs. Bot. 4: 22 (1786).

Vahlia oldenlandioides Roxb. Fl. Ind. 2: 89 (1832); Hooker f. & Thomson, Journ. Linn. Soc. 2: 74 (1857); Oliver, Fl. Trop. Afr. 2: 384 (1871); Hutch. & J. M. Dalz. Fl. W. Trop. Afr. 1: 106 (1927).

V. oldenlandiae DC. Prodr. 4: 54 (1830).

V. tomentosa DC. *l.c.*

V. ramosissima DC. *l.c.*

V. cordofana Hochst., Flora 24 (1): Intell. 43 (1841).

V. macrantha Klotzsch in Peters, Reise Mossamb. Bot. 175 (1862).

V. dichotoma (Murray) Kuntze, Rev. Gen. 227 (1891); Keay in Hutch. & J. M. Dalz. Fl. W. Trop. Afr. rev. ed. 1: 120 (1954).

V. pentandra (Retz.) C. E. C. Fischer, Bull. Misc. Inf. Kew 1932: 56 (1932).

Bistella digyna (Retz.) Bullock, comb. nov.

Oldenlandia digyna (Retz.) Obs. Bot. 4: 23 (1786).

Bistella geminiflora Del. Cent. Pl. Afr. 7 (1826) & Voy. Méroé 2: 97, *t. 2, fig. 2* (1826), *typus nominis generici.*

Vahlia weldenii Reichb. Ic. Bot. Exot. 1: 62, *t. 91* (1827); DC. Prodr. 4: 53 (1830); Boiss. Fl. Orient. 2: 799 (1872).

V. sessiliflora DC. *l.c.* 54.

V. silenoides DC. *l.c.*

V. viscosa Roxb. Fl. Ind. 2: 89 (1832); Hooker f. & Thomson, Journ. Linn. Soc. 2: 74 (1857); Oliver, Fl. Trop. Afr. 2: 383 (1871); Hutch. et J. M. Dalz. Fl. W. Trop. Afr. 1: 106 (1927).

V. digyna (Retz.) Kuntze, Rev. Gen. 227 (1891); Keay in Hutch. & J. M. Dalz. Fl. W. Trop. Afr. rev. ed. 1: 120 (1954).

V. menyharthii Schinz, Bull. Herb. Boiss. Sér. 2, 2: 944 (1902).

V. somalensis Chiov. Fl. Somala 170 (1929).

V. goddingii Bruce, Bull. Misc. Inf. Kew 1940: 49 (1940).

Bistella capensis (Linn. f.) Bullock, comb. nov.

Russelia capensis Linn. f. Suppl. 175 (1781), *typus nominis generici.*

Vahlia capensis (Linn. f.) Thunb. Nov. Gen. Pl. 2: 36 (1782), *typus nominis generici*; DC. Prodr. 4: 53 (1830); Harvey in Harvey & Sonder, Fl. Cap. 2: 306 (1862); Oliver, Fl. Trop. Afr. 2: 384 (1871); Hiern, Cat. Afr. Pl. Welw. 1: 324 (1896).

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FROM BOTANICAL BIOGRAPHY TOWARDS ANIMAL ICONOLOGY

FRANS VERDOORN [1]

(Biohistorical Institute of the University of Utrecht)

(received December 10th, 1965)

This essay is mainly a restatement of the biohistorical ideology such as we developed it during recent years. At a recent international congress, I tried to present this in a detached, logical way (1965). At other times, I endeavoured to clarify it by using a case history (1964). In both cases, certain things remained unexplained and I will now try to elucidate the development of our biohistorical ideology along somewhat different lines. In doing so I shall avoid unnecessary personal reminiscences, but some facts of a personal nature or relating to the development of our Institute necessarily will have to be recapitulated in this connection. Many factors are involved, ranging from the increase in our staff, to the augmenting interests of our students (which forces us to pay some special attention to their education and, just as any editor will learn much through his editorial activities, one learns so much more by teaching than I formerly understood or expected). Other factors again are the increase of our library holdings and documentation programme, talks with colleagues (particularly in the literary faculty) and those visitors from abroad who do not come only — welcome as they are — to copy certain data from various sections of our *Index Ultrajectinus* (a world index of the literature of biohistory, entirely separate from our Library Catalogue).

Then, one makes schemes which frequently do not materialize rightaway, but which nevertheless are most helpful in planning for the future. As to our ideology, there is very little new in it, if considered from the point of view of the great medical humanists of the past. The materia medica, however, is only partially identical with the materia biologica and it took me many years to apply the ideology of the medical humanists to our own subject matter. Most medical historians always considered it a very natural thing to enter a variety of humanistic pastures and, whenever their rambles went beyond the traditional fields of history *s.s.*, they never felt an urge to employ another term for whatever they were doing than "history of medicine".

I just wrote about a restatement of our biohistorical ideology — before there was any reshaping to be done, we underwent a formative period and I must acknowledge, in this connection, what we learned from many medical historians in New England (particularly the medical members of the Boston Biohistorical Club) and others in centres at Yale, Manhattan, Baltimore's Johns Hopkins, and Washington, D. C. Why was it that in reshaping a club, which since the days of Harvey Cushing had never felt the need to call itself otherwise than the "Boston Medical History Club", the need was felt to employ the term "Biohistory" (a term of which we knew that it had been employed in the past occasionally in various other senses, such as phylogeny, etc.)? As it came to happen, a group of workers in the life sciences with humanistic interests — where man is both a subject and an object — joined forces with an existing nucleus of men of medicine. To the average biologist "history" means "history *s.s.*", and if he tries to extend his historical interest, he mostly enters theoretical biology or some related field of the philosophy of biology. As our interests were different, we felt the need for another term which since has been utilized by several others, in the U.S.A. and Europe.

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[1] *Communicationes Biohistoricae Ultrajectinae 5.*

In these and following considerations, I will avoid the mention of personal names in order not to sun myself in the fame of many men of renown, but an exception should be made for the late George Sarton to whose kindness my wife and I owe so much, to the late Dr. E. D. Merrill who, whenever he wished, was not only a great taxonomist, but also an astute citizen in the republic of letters (1946 & 1954), to the late Dr. H. E. Sigerist and, particularly also, to two men I never knew personally, Charles S. Sargent, the founder of the Arnold Arboretum, and to the Swiss zoologist, the late Prof. R. Burckhardt.

It was in the early 1940's, shortly after settling in the U.S.A., that I found the Arnold Arboretum Library at Jamaica Plain, Mass., a wonderful place to gather further data for a project started before the Second World War, the *Index Botanicorum*, a biographical dictionary of plant scientists of all types and all periods (VERDOORN, 1937 & 1944). With the aid of the resources of the Arnold Arboretum, an interleaved copy of the second edition of Pritzel's *Thesaurus Literaturae Botanicae*, with which my wife and I had started gathering biographical data, was soon extended to a fairly extensive card index by combing journal after journal, and book after book.

In doing this, I received much help from various staff members of the Arnold Arboretum, such as Capt. V. C. Asmous, Dr. L. Croizat, Mrs. J. Sellars, Dr. A. Rehder, Dr. A. C. Smith, and, later particularly also, from Mrs. Lazella Schwarten. At one time, in the mid-1940's, in addition to my wife and Mr. K. W. Baron, five typists were busily copying and compiling—in not too large a house at Waltham, Mass.—what is now the *Index Biographicus* of the *Index Ultrajectinus* of the Utrecht Biohistorical Institute.

Many of those who worked at the Arnold Arboretum, its Herbarium and Library, were primarily or exclusively concerned with taxonomy and not always realized that they were working in an institution built up by a man, the late Charles Sprague Sargent, who was — to phrase it as briefly as possible — if not a botanical, at least a "dendrological Osler". For many years, I too, was not too much aware of this, for my approach to the history of the plant sciences and related subjects was very much along biographical lines. A feeling that man as the maker of the science of plants is an extremely important factor in the history of the plant sciences was forcefully instilled in many of his students by the late Prof. F. A. F. C. Went who taught his pupils, time after time, illustrating his views with a variety of examples, frequently derived from current work in experimental stations in the former Netherlands East Indies, that plants alone do not yield a grain of botany, but that man, the maker of botany, is a factor without which botany would not exist and also, that it is utterly foolish to make a sharp distinction between the pure and applied plant sciences (VERDOORN, 1938). This, of course, applies to many fields of science and learning and is hardly a very original idea which will seem very childish expressed to colleagues in the Interfaculty. Yet, I never had an other teacher who returned, time after time, to this subject in his courses for graduate students and who, via the first series of *Chronica Botanica* (which was only concerned with man as a factor in current and projected plant science research), made me turn to botanical biography which is still very close to my heart and to which the largest division of our Institute is devoted.

To return to the Arnold Arboretum, in its rich and well organized library I gradually found much more — as one may well expect in the heritage of a "dendrological Osler" — than data for the *Index Biographicus*. On the one hand, my interest in botanical gardens and arboretums, both their history and ideology, somewhat latent since I had the opportunity to work in our *Hortus Bogoriensis* in 1930[2]) — was revived and for many years, the past, present and future of botanical gardens received much attention (VERDOORN, 1948 & 1953). World indices were started as well as a collection of books etc. which one now finds in the Bio-Topographical Division of our Institute. With the idea of building up something like the Sargentian heritage, I acted as organizing director of the newly established Los Angeles State and County Arboretum during 1948/1949 (VERDOORN, 1948) which was a most interesting experience during which I made a "master plan" and also learned the difference between the American West of fiction and of fact. Whenever time permitted, a variety of data were gathered in the wonderful Huntington Library at San Marino.

At least as important where the "discoveries" subsequently made in a number of minor library sections built up by C. S. Sargent, ranging from travelogues to works on trees in creeds and religions, and from the influence of deforestation on world history to wood utilization through the ages. Though realizing that many of these subjects were interrelated or, at least, had some bearing on each other, it took me quite some years to coordinate all this[3]).

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[2]) I should admit that my interest, at that time, was mainly in scraping hepatics from the barks of trees and observing the enormous influence of such factors as light and humidity on the variability of hepatics.

[3]) I recall how George Sarton, who had never visited the Arnold Arboretum Library before, said—ca. 1947, during a visit there by the members of the Tannery Club—something like "amazing . . . so many humanistic aspects represented in a botanical institution". This was long before I was truly aware of the essential

Books, card indices, and all kinds of other biohistorical documentation first filled one house in Waltham, Mass., then a second one. It was at this time, in the mid-1950's, that Prof. Lanjouw was instrumental in enabling me to set up a University institute at my *Alma Mater.* I am well aware that many American friends felt that this could have been accomplished by joining forces with one of their medico-historical institutions. Important as early medicine may be to us, I wanted, however, to set up a biological institution. Some Utrecht University authorities were, initially perhaps, mainly thinking in terms of teaching the traditional history of the organic sciences. This is being done, not only bij offering a course, etc. in biohistory, but also by making it possible that post-candidate students can work at our Institute during either 3, 6, 9, or 12 months towards their doctorate, an opportunity which exists in very few biological (sub) faculties throughout the world. Biohistory, however, offers those, who desire so, a variety of other exciting possibilities.

Several years before I was enabled to set up the Utrecht Biohistorical Institute, it dawned on me that the interrelationships between the life sciences (incl. certain aspects of chemistry, and a good amount of medicine) and the humanities were essentially different, or at least have an entirely different spectre, than we find in the exact sciences or in science considered as a whole. I wrote previously about this, but now feel that I did not make things too clear, either in an address prepared for the Florence Congress of the History of Science, etc. (Verdoorn, 1951 & 1956) or my inaugural address at Utrecht (1958) as I was still thinking too much in terms of historiography, biography, bibliography. etc.

By teaching, by collecting, by abstracting, and above all, by the freedom allowed by the Netherlands academic tradition, it gradually became clear to me that my original definition of biohistory as "the history and related humanistic aspects of the life sciences" should be more properly replaced by "*the historical relationships of plants, animals, and man in science, early medicine, and culture*". According to this principle we now distinguish 7 primary branches of biohistory, for most of which we are developing a division, *sc.*:—

1) *The Formative Periods.* The history of the interrelationships between plants, animals, and man (from the Palaeolithicum through the Middle Ages) is extremely interesting as during most of these periods languages, creeds, literature, art, plants and animals in daily life, as well as medicine, were more closely interrelated than during later periods. The special aspects of the Hellenic period should be

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differences between the humanities and science and the problems involved in the possibilities of bridging the two. The removing of the unique Sargentian Library from Jamaica Plain, Mass., to Cambridge, where it was incorporated with other collections and where its charming and stimulating open stock nature was lost —I am certain with the most honest intentions of those involved—nevertheless was felt as a cruel act by many.

recognized, as well as the fact that no research of any of these periods can be undertaken unless the languages concerned[4]) have been properly mastered.

2) *The Life Sciences, early Medicine, etc., during the Renaissance and later periods.* I wrote previously (e.g., 1944, 1951 & 1963) in detail about a variety of aspects of the history and historiography of the life sciences, particularly its methodology, biography, bibliography, the history of the applied plant sciences, garden history, etc., and will not summarize these views again (cf., however, some of the concluding remarks). I may only add that, as per our understanding with the Utrecht Institute for the Philosophy of Science, we will in general restrict our programme, as far as the philosophical aspects are involved, to (a) the interrelationships between the history of philosophy and the history of the life sciences, (b) the history of concepts in theoretical biology, etc., and (c) the philosophy and methodology of historiography.

3) *The Ethnological Aspects* (post-mediaeval & comprehensive). We have quite some documentation on ethnobiology, folklore, etc., but are reluctant to enter into research in social anthropology, a field which greatly developed in recent decades (which, i.a., would call for adding a motif index to the *Index Ultrajectinus*). It should be recognized that which is called "ethnobotany", etc., in many institutions of systematic biology touches only on certain, though basic, aspects of this and I should like to quote briefly from ARMSTRONG's (1964) latest definition of folklore (with special reference to birds — in which the term folklore, however, is applied in an unusually broad sense):

> "A branch of social anthropology dealing with data in which birds figure, including local names, proverbs, legends, myths, folktales, rituals, and symbols. Aspects of the human exploitation of birds, such as devices for trapping them and the use of their plumage as adornments or parts of their bodies as medicine, are also relevant. Hunting and fowling were the mainstay of life in Palaeolithic times, and traces of beliefs and rituals concerned with increasing the fertility and vulnerability of prehistoric man's quarry survive in extant traditions. Thus folklore is indispensable as one of the few sources of information concerning the modes of thought and spiritual life of earlier communities. The importance which preliterate peoples attached to birds as beings possessing supernatural powers is attested by cave art, wherein men are represented with bird-like heads—probably masks, and by the myths in which birds participate in creation or have vital cultural roles attributed to them".

4) *Biocontrol* (post-mediaeval & comprehensive). We had to coin this term for the history of man's domination of nature, a variety of

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[4]) For this reason, we concentrate to some extent on the Palaeolithicum-Neolithicum (which will call for a biohistorical laboratory), on the Ancient Far East (many holdings, but no sinologist, as yet), and the Middle Ages (both as Utrecht University is a great centre for mediaevalistic studies and as this period is very important to our "Bio-Symbolon Workgroup"—we realize that some knowledge of Greek and Latin, a slight knowledge of Arabic and the ability to utilize various dictionaries of late Latin, and other mediaeval languages are utterly insufficient, but this period is biohistorically of such a tremendous interest that a staff able to cope with it just will have to be built up).

subjects, frequently and confusingly interpolated in dealing with the history of the life sciences. It includes such subjects as the history of man-land relationships, certain aspects of the history of domesticated plants and animals, the history of hunting and fisheries, nutritional history, "disease and civilization", the very extensive history of biotechnology, etc.

5) *The Literary Aspects* (mediaeval, later & comprehensive). Our medical colleagues have always been much interested in these, and oak-paneled rooms filled with novels and poetry, by and about physicians, as well as didactic poems, etc., will be found in many of the large medico-historical institutions. The same type of literature exists about plants and animals, and to a much minor degree than in medicine, biologists have entered the domain of the "belles lettres". This, however, is only one aspect. At least as important from our point of view is the literature in which animals (and to a minor extent plants) play a symbolic role. The prototypes of this type of literature, incl. much mythological, sacred and devotional literature, frequently date back to the formative periods. *These myths, early religious concepts, bestiarii, fables, emblemata texts, etc., are a most typical example of what is considered of the utmost importance in one faculty and may seem utterly foolish to many in a faculty concerned with stellar physics and molecular biology.* It should also be recalled that this type of literature is not only of importance for its own sake, but also both to those concerned with the ethnological and particularly with the art historical aspects.

6) *Art Historical Aspects* (mediaeval, later, & comprehensive). Many biotaxonomists claim to be interested in these, but in general they refer to the graphic arts (as exemplified, let us say, by Gould or Redouté), to typographical history, etc. It is true, Gould and Redouté were great artists, but their importance is mainly iconographical (*s.s.*) and not iconological, i.e., without a spiritual meaning. I hardly need to say that the graphic arts, in their multivarious aspects, greatly concern and interest us. Some of the most interesting problems in biohistory, however, are concerned with the symbolism of plants, and animals, as well as with pharmaceutical and medical representations in mediaeval, Renaissance and Baroque art. Long ago, I used to spend many a Saturday afternoon gathering data mainly relating to plants and horticulture, along these lines, in Harvard's Fogg Art Museum. Then, I turned to those few icones of certain emblemata in which plants are of some real importance, etc. Gradually, however, it became clear that animals as symbols, attributes, allegories, etc., have been a tremendously more important aspect of civilization, through the ages, and that much of it is still obscure. One needs a knowledge not only of systematic zoology, but occasionally also of such unexpected fields as endocrinology, etc., in addition to a thorough knowledge of the literary sources, sacred and profane, a perfect understanding of the many facets of symbolism (the unspoken language of the ages, from the mesolithic rock paint-

ings to the folk prints of scarcely a century ago), and above all of "l'imagerie de l'art chrétien médiéval".

7) *The Linguistic Aspects* offer the properly trained biohistorian intriguing problems with which, at present, we just cannot cope in spite of the fact that we gathered a good collection of "natural history" and related dictionaries of all types (arranged chronologically until 1900, and alphabetically by authors after 1900). We also gathered a good number of etymological studies, but ever since I went through such works as *Gottfried's Pelzbuch* by Eis or *Die Deutsche Vogelnamen* by Suolathi, I have felt that this subject matter can best be tackled by biohistorians in cooperation with properly trained linguists, in which the latter should have the last word5). Of particular interest also is the very early history of writing in which plants and animals are frequently represented, both to identify them as well as symbols.

According to its title, this essay should now come to an end; yet, I may be permitted a few final remarks.

In history, particularly in biography, the formative and causative factors are often overlooked with the result that by neglecting the matrical factors6) a very one-sided and non-analytic picture is frequently given. To the historiographer of early botany, it may not mean much that, e.g., Ernst Meyer, throughout his life was deeply influenced both by Albertus Magnus and Goethe, yet, his classic *Geschichte* cannot be properly appreciated unless one is well aware of this. This is just one example; *giving proper attention to the matrical factors, whatever the subject, is not only essential in, but the essence of biohistorical work.*

To return once again to bio-symbolism, the *Physiologus* is hardly a classic of animal science (though it yields some unexpected data). Biohistorically it is a mos interesting example of the fact that one has to be familiar both with literary history of a great variety of types (incl. the canons of the great religions), with art history (particularly iconology), and, last not least, with certain aspects of social anthropology, each of which may derive again profit from work in a related field. To which extent such "scientific oddities", in a related field, played an enormous role in cultural history has recently been analyzed by Dr. H. M. E. de Jong (1965).

In the meantime various subjects, such as biography, bibliography, historical biotopography, which I considered at one time as "prime branches" of biohistory, now appear only methods or aspects of historiography, etc. It should, however, be emphasized that they often call for very *extensive reference divisions* operating according to the special methods involved in which connection our Biographical Division, in the long range, will continue to have priority.

Then, considering our Institute and our developmental plan, we have or need certain divisions serving our Institute as a whole (the *Index Ultrajectinus*, with minor exceptions, e.g., can be maintained only

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5) The dangers of "wisdom without understanding" resulting from a one-sided approach have been outlined, in this connection, often rather caustically, by the late Dr. E. D. Merrill (e.g., 1946 & 1954).

6) An other term for which I felt a distinct need.

centrally). On the other hand, there is a need for certain special work or study groups (such as our Bio-Symbolon Workgroup and our "Dutch Golden Age Study Group", i.e., the Leeuwenhoek Commission, etc.). I also did much preparatory work towards a study group for the history and technique of international relations in the life sciences in a detached and academic way, etc. Some of these work or study groups may operate entirely within the framework of the Biohistorical Institute, but mostly they will call for interfacultary, national or international cooperation.

Then, a biohistorical serial must be started as soon as proper care will have been taken of certain arrears and, sometime in the 1970's, an international advanced course in biohistory should be added to our educational programme.

"History, etc., should not be a goal by itself, but a tool for the present" claim some historians (occasionally quoting such dicta as Fr. Bacon's "itaque ipsissimae res sunt . . . veritas et utilitas"). This will often hold true, but as a categoric statement, it sounds rather Hitlerian. As to biohistory, some projects will be purely academic, whereas others may be of a tremendous help to a variety of workers in non-historical fields. *A properly balanced biohistorical institute, at the same time, can be a most useful documentation centre for sundry workers in the life sciences* (to which we are giving much thought and attention in connection with the transfer of our Institute — sooner or later — to the "Uithof", the new campus of our University in a suburban area near de Bilt). Yet, whatever the use of pinpointing publication dates, biographical dictionaries, special subject bibliographies, etc., may be, it seems more important, as Sigerist often pointed out, that history, etc., can permit us to bring certain humanities close to the scientists and to teach a scientific outlook to the students of certain humanities in a language that both can understand, broadening their horizon and preventing them from becoming narrow specialists[7]). Ceterim, what is the "use" of music, what is the "use" of art . . . ?

In concluding I must point out that it cannot be helped that some projects, for which my wife and I previously gathered much material, have occasionally, to some extent, temporarily been replaced by other projects (for which less material was gathered). It should also be understood that I gradually revised our programme, both according to the resources of Utrecht University (scant in some ways, on the niveau of the best universities of the world in other cases) and the abilities of our devoted staff (now consisting of some eight members, most of whom were chosen on account of their potentialities besides their immediate abilities), as well as the hon. research fellows of the Int. Biohistorical Bureau, in the hands of all of whom rests the future of what we started and who join in paying tribute, at this occasion, to the initiative taken by Prof. Lanjouw.

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[7]) This sounds as nice as it is difficult (particularly in continental universities which are mostly of the "graduate school type"; in general, resulting in unavoidable compartimenta).

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A REASSESSMENT OF THE CYPHELLACEAE[1])

M. A. DONK
(Rijksherbarium, Leiden)

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A suitable subtitle for this paper would have been "The rise and fall of a family". What is usually called the *Cyphellaceae* is an instructive example of a situation not uncommonly encountered in the current systematics of mycology: a family retained in a traditional sense by some mycologists and considered by them as good a family as any, while others are convinced that it is nothing but a handy bin from which part of the contents has already been taken out and disposed of by scattering it over various groups, but which is still needed for keeping what remains. We do not yet know what to do with this considerable remainder, mainly because the published accounts are inadequate and the species have not yet been scrutinized anew in the light of present-day taxonomic requirements.

In order to understand the basic idea of the *Cyphellaceae* the type species may be briefly introduced. The fact that *Cyphella digitalis* was originally described as *Peziza digitalis* is telling, and one could not do better than characterize it as a 'discomycete' with basidia, viz. a cup-shaped fruit-body with the hymenium lining the smooth inside or 'disk'. If one were pressed to form an opinion about its taxonomic position from a dried, not annotated collection and without the aid of the microscope, one would even now, very likely, dispose of it as a discomycete. However, there is little doubt that in nature the cup is directed downward at least when mature, in contradistinction to the average discomycete in which the hymenium containing the asci is directed upward. This difference is a reflection of the two modes of violent spore discharge inherent in the hymenomycetous basidium and ascus; it has been explained through Buller's well-known researches. The cups in the various species are not always typically cup-shaped; in a number they are more or less tubular or else more flattened and even disk-like.

Once their true nature was recognized these discomycete-like basidiomycetes had to be reclassified in the system of the *Hymenomycetes.* Since the hymenium is smooth, the '*Thelephoraceae*' became the receptacle for the species with more or less scattered fruitbodies (*Cyphella*). In other species the fruitbodies may be so densely crowded that together they simulate the pore layer of the '*Polyporaceae*'. In *Solenia* (correct name, *Henningsomyces*) the 'tubes' are seated directly on the substratum. In *Stromatoscypha* (originally *Porotheleum*) they are

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1) This paper is an adaptation of the text of a lecture delivered at the Third European Mycological Congress, held in Glasgow.

crowded on a well-defined membranous stroma, common to a colony. Hence these fungi became to some authors members of the '*Polyporaceae*'.

This was, roughly, the situation when PATOUILLARD (1900), after preliminary steps by Quélet and Schroeter, decided to assemble these discomycete-like *Hymenomycetes* into a taxon (subtribus) of their own. He admitted the genera *Aleurodiscus*, *Cytidia*, *Cyphella* (fused with *Solenia*), *Porotheleum*, *Punctularia*, and *Phaeocyphella*. Later mycologists usually kept to Patouillard's circumscription except for some minor alterations, such as the exclusion of *Aleurodiscus*, and still more unanimously, of *Punctularia*. After some time the taxon was raised to the rank of a family, a simple definition of which runs: tube-, cup-, or disk-shaped fruitbodies with the smooth or slightly wrinkled basidial hymenium lining the inside, viz. the concave to flattened or even slightly convex disk.

The assignment of *Punctularia* to the cyphellaceous fungi was unexpected. Patouillard was the first to discover that the knobs and folds of the hymenial surface (often likened to that of typical species of *Phlebia*) of the resupinate fruitbody were not really what they appeared to be, but were distinct cushions covered by the hymenium and separated by narrow, sterile troughs. This led him to conceive the only species he knew as comparable to *Stromatoscypha* but with convex rather than concave individual fruitbodies seated on a common subicular layer.

It sometimes does not take long after a family has become established to attract elements that tend to obscure its original character: it then grows out *par enchaînement*. This happened in this case, too. Thus, *Fistulina* was assigned to the family. Another introduction was *Chlorocyphella*, believed to be a lichenized cyphella. At a much later stage followed the genera *Campanella*, *Leptoglossum*, *Arrhenia*, *Rimbachia*, and *Flavolaschia*. In this way various elements were added that considerably departed from the straightforward original conception: for instance, some of these elements had laterally stalked caps, and others a strongly veined to almost lamellate or even tubulate hymenium. With these additions the family was raised to the rank of a suborder and divided into three families, *Cyphellaceae*, *Leptotaceae*, and *Fistulinaceae*. However, none of these innovations has found much general support.

Let us briefly examine some of these accretions. As soon as a relationship between two groups of the magnitude of rather diversified families is postulated it is apt to become a two-way traffic bridge. This is what also happened in connection with the *Polyporaceae*, of which *Fistulina* has been considered a good example by many mycologists up till to-day.

Persoon was the first to compare *Solenia* (*Henningsomyces*) with the resupinate species of *Polyporus* (viz. the modern artificial genus *Poria*). The separate fruitbodies are often elongate to cylindrical and when densely arranged they do closely resemble porias. Fries went a step further and classed *Solenia* as well as *Porotheleum* (*Stromatoscypha*) in the *Polyporaceae*. The theoretical implication behind this was that *Solenia* had free tubes represented by the individual fruitbodies which are directly seated on the substratum; *Porotheleum*, free tubes on a quite distinct, membranaceous subiculum common to the whole colony; and that in *Fistulina* the subiculum was replaced by an extremely well-developed laterally stalked fleshy-fibrous and succulent cap, but all the same also bearing free tubes. The bridge that served Fries to transfer *Solenia* and *Porotheleum* to the neighbourhood of *Fistulina* and into the Polyporaceae has been used by some modern authors to transfer *Fistulina* into the *Cyphellaceae*.

Another quite remarkable two-way bridge is between the *Cyphellaceae* and the *Corticiaceae*; it may be called after *Aleurodiscus*. This genus has gradually become more and more a storehouse of corticiums with some kind, any kind, of so-called paraphyses. It is not this artificial genus *Aleurodiscus* I have in mind, but the one as recently redefined, in which the development of the basidia and amyloid spore-wall play an important role in the generic character. The type species is *Aleurodiscus amorphus*, originally held to be a small cup-fungus: in outer appearance it is certainly like a discomycete and hence cyphellaceous. If one gradually extends the genus *par enchaînement* it appears quite justifiable to penetrate more and more into the crowd of cyphellas and to enlist in *Aleurodiscus* such fine, big, cup-shaped fungi like *Cyphella vitellina* from South America. One also realizes to his astonishment that the very type species of *Cyphella* itself (*C. digitalis*) is in certain features very similar to these cup-shaped species of *Aleurodiscus*. Patouillard was quite correct, one would conclude, to make *Aleurodiscus* a genus of the '*Cyphellaceae*'. However, surveying the species of *Aleurodiscus* in another direction one soon comes across such species as *A. aurantius*, a fungus with completely 'resupinate' (effused) fruitbodies and in all respects ideally corticiaceous and belonging to the '*Thelephoraceae*' of the traditional classification. It was natural that some authors placed *Aleurodiscus* in its entirety, as well as *Cyphella* reduced to its type species, in the '*Thelephoraceae*' or in a segregate thereof, the *Corticiaceae*—and thus excluded *Cyphella* from the '*Cyphellaceae*'.

Another example is the *Leptoglossum* bridge. *Leptoglossum* reminds one of *Aleurodiscus* in so far that it is partially typically cyphellaceous in the traditional sense. The smallest of its species (let us call it *Cyphella muscicola*, but this is not the correct name) is more or less cup-shaped, and has a smooth hymenium. It very closely resembles young fruitbodies of *L. retirugum*. Next come the species that have been placed in a distinct genus *Leptotus*, now fused with *Leptoglossum*. They are *Leptoglossum retirugum* and *L. lobatum*; both are initially dorsally attached and finally attain far bigger dimensions and have a pronounced tendency to throw their hymenium into folds which may become radially arranged and in appearance somewhat gill-like with cross-veins. Then follows *Leptoglossum muscigenum* with a distinct but short lateral stalk; then *Omphalina rickenii* with erect, centrally stalked fruitbodies and folds well enough developed to include it in the agarics; and finally we arrive at *Pleurotus acerosus* with gills in *optima forma*. All these species have the same hyphal structure, the same general form of spores of about the same dimensions; the same brownish or greyish-brown colours with corresponding membrana-pigments encrusting the outer hyphae; and the same habitat, for they are all moss-loving. The series appears so perfectly coherent that all its species are now placed by some authors in the single genus *Leptoglossum*.

So far about some examples of the relatively late influx of genera which do not well conform to the traditional character of the *Cyphellaceae*. On the other hand it has not yet been fully realized that if a broadly conceived family of Cyphellaceae is to be maintained, the genus *Schizophyllum* has carefully to be weighed for admission. It is now classed as a genus of gill-fungi but this is not correct. The so-called split gills which characterize the genus are morphologically not at all comparable to the gills of the agarics. The fruitbody is in origin typically cyphellaceous but soon it becomes complicated by proliferation of radially outgrowing marginal lobes. Two adjacent sides of two grown out marginal lobes pressed together form together a 'split' gill. In addition adventitious split gills may also be formed in the hymenial surface.

But let us return to the more restricted and traditional circumscription of the family and recall a diagram published in 1925. It expressed the phylogenetic relationships as they were thought likely by its author. How important this family looks from an evolutionary point of view! It appears as a knot that connects various lines of evolution, viz. (i) toward the *Polyporaceae* through *Stromatoscypha*, (ii) toward the *Cantharellaceae* through *Leptoglossum* (iii) toward the Hymenolichens through *Chlorocyphella*, and (iv) from the *Corticiaceae* in a wide sense through such genera as *Cytidia* and *Cyphella*. Can this scheme stand the test of time after 40 years?

Before answering this question it may be pointed out that some of the genera should never have been included. Apparently they were unknown to the maker of the diagram from personal experience. *Chlorocyphella* has no basidia; it is a genus of imperfect fungi or lichens. Thus, any connection with the Hymenolichens must be given up. The presence of *Hypolyssus* in this scheme is based on a palpable error and it should be left out of further account, too.

As we saw, accepting a close connection with the Polyporaceae is very tempting indeed. Still less difficult is assuming close connections between such genera as *Cytidia* and various *Corticiaceae*, particularly if one places *Aleurodiscus* in the latter family. As to the relationship with the *Cantharellaceae*, this was suggested by the wrinkled or veined hymenium of some species of *Cyphella* when well developed, and by taking the *Cantharellaceae* in a broad and artificial sense. If one restricts that family to those species of *Cantharellus* and *Craterellus* with stichic basidia, then any relationship with the *Cyphellaceae* becomes difficult to defend. However, the *Cantharellaceae* may well be replaced in discussions by the *Agaricales*, for *Leptoglossum* is obviously closely related to some species that are definitely typical agarics rather than species of *Cantharellaceae*. Thus, there should be little doubt that if the naturalness of the *Cyphellaceae* is postulated it would be outstanding for its many-sided relations to various other families.

If the *Cyphellaceae* were a natural group . . .! The same situation could theoretically also readily be explained by assuming its artificiality. If one includes in a single family the kangeroo, the kangeroo rat, and other leaping mammals and considers them to form a natural taxon of closely related genera, one will get a situation comparable with what has been inferred for the *Cyphellaceae*.

Both the cupulate habit and the smooth hymenium that are the leading characters of this family may be explained as end stages in processes of reduction. Although the typical agarics are centrally stalked, many groups include elements with cupulate fruitbodies, a phenomenon that is coupled with the substratum, viz. stalks of plants, stems of trees, rotten wood, leaves, mosses, instead of the ground. It is also plausible to derive orbicular, but strictly effused, fruitbodies of the *Corticium* type through appressed-peltate ones, from the flattened cupulate fruitbody of 'cyphellaceous' genera as *Cytidia*.

The cyphellaceous or discomycete-like habit is encountered in practically all groups of *Hymenomycetes*; thus, the *Auriculariaceae* have the genus *Hirneola* (the Jew's ear); the *Tremellaceae*, *Exidia*; the *Dacrymycetaceae*, *Femsjonia*. If no special attention had been paid to their basidia these genera might well have been included in the *Cyphellaceae*, too. This shows that the cup-shaped fruitbody has originated along many convergent lines of development.

Even when the cupulate habit is not in evidence in the fully developed fruitbodies of certain agarics it still may occur in the initial stages. A good example is *Pleurotus* (= *Phyllotus*) *porrigens*. If the fruitbody initials were to stop growing out at a very early stage, a good cyphella would result. Would the derivative be the type of a new genus? That depends on what one would know about its genesis. Those who would know how the derivative came into being would presumably call it a new, much reduced species of the same genus; those who would not be informed about the actual relationship would be likely to place it in a different genus and perhaps even in a different family. The situation that one is actually aware in advance about the genesis of such a derivative is hardly ever realized and the taxonomist will have to fill up this gap in his knowledge by acting as a detective and gather his evidence from a detailed examination of his material, mainly by carefully studying the microscopical and chemical features.

The very existence of such series as *Leptoglossum* and *Aleurodiscus* is proof of the existence of the process of transmutation from one ecological type into another. In the *Leptoglossum* case the transmutation of the shape of the fruitbody goes hand in hand with the transmutation of the hymenium from lamellate to smooth, or vice versa. Another example of such a series, this time a very short one is *Mniopetalum*—if it is really a natural unit. It contains two cupulate species of which one (*Mniopetalum globisporum*) has s smooth hymenium and the other (*Agaricus bryophilus*) a typically lamellate one.

Considerations like these have lead to the working thesis that the *Cyphellaceae* is a standard example of an artificial family, and that as much of its contents as possible should be driven out along all the available as well as several new bridges to other groups of *Hymenomycetes*. Some of these bridges impress one at the moment as well-constructed and solid; others appear still rather ramshackle; and still others are positively perilous, or still under construction.

One of the main difficulties which has to be attended to preceding an orderly exodus is unmixing the cocktail: all of the few traditional genera appeared thoroughly artificial, too. A lot of splitting up and re-classifying into smaller genera has recently been done and has resulted in about twenty or so new genera. This process is still taking its course and with it the rapid deflation of the family. As yet it is not possible to predict that some of the residual contents consist of one or more smaller independent families.

The intention of this paper is not to discuss one by one all groups that have absorbed former elements of the Cyphellaceae. A brief mentioning of some examples additional to those already mentioned may suffice. One of the earliest, and now rated as one of the safest, is the bridge through which *Lachnella* (in a strongly emended sense) was driven out to occupy a position in the neighbourhood of the agaric genera *Chaetocalathus* (cupulate) and *Crinipellis* (centrally stalked). In its wake follow *Cyphellopsis* and perhaps still other genera. The fusiform bodies occurring in the hymenium of *Lachnella villosa* and other species are in my opinion young basidia rather than cystidioles. Exactly similar basidioles are very rare among the agarics except in some groups with one of which *Lachnella* is now actually associated.

Resupinatus is an agaric genus with small to minute cupulate fruitbodies. If one takes away the gills, which may be few, one has constructed species that would find their place in the cyphellaceous genus *Stigmatolemma* as recently emended, redefined, and excluded.

The outside of the fruitbody of the cyphellaceous genus *Calyptella* is occupied by appressed hyphae which form botryose or simpler patent excrescences. The same structures we find also in some of the non-amyloid spored species of the agaric genus *Mycena*; the resemblance of the total of microscopical and chemical features is so suggestive that a close connection between the two genera may be accepted as very likely.

In many of these fungi with so strongly reduced fruitbodies the most important characters are often to be found in the hairs (terminal cells) clothing the outside of the cups. The number of genera that can be recognized by a close and detailed study of these hairs is rapidly increasing. Most of them are suspected to be related to such genera as *Marasmius* and *Crinipellis*. One sometimes feels like a pedlar going from genus to genus, from door to door, with his often limited notes to find response. In those groups of agarics where, for instance, the microscopical details of the cap are well studied one will succeed occasionally, but contact cannot be established except when the details at both sides are worked out rather carefully and extensively.

What will happen to the original type genus of the '*Cyphellaceae*'? After it was excluded it was disposed of as part of, or placed in the neighbourhood of, *Aleurodiscus*, a genus that itself was stowed away for convenience's sake in that artificial assemblage now called *Corticiaceae*, a name which for nomenclatural reasons is likely to be suppressed in the future. And when its contents are reclassified a mycologist will come across the genus *Cyphella* to which an early family-name is tied. I certainly would not be surprized if the name were to be taken up again to act as a crystallization centre for a family very different from the one that was originally called by exactly the same name. It may well happen that within a few years we will be able to watch the rise of a family of *Cyphellaceae* once more.

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THE GENUS MATHEWSIA (CRUCIFERAE)

REED C. ROLLINS

(Gray Herbarium, Harvard University, Cambridge (Mass.) U.S.A.)

(received October 15th, 1965)

Among the endemic and sometimes localized genera of the *Cruciferae* occurring in South America, *Mathewsia* stands apart as an element of the distinctive desert flora of southwestern Peru and western Chile. As far as present records show, the genus is confined to a relatively narrow strip wholly west of the main Cordillera, not far from the Pacific Ocean. Some species are confined to washes or small arroyos known as quebrades. Others occur as part of the lomas vegetation of western Peru. Populations of the same species occupying different quebradas often differ from each other to a limited degree and in many instances probably little or no gene exchange occurs between them. The intervening dry areas, separating one quebrada from another, are completely unsuited to the growth of *Mathewsia* and form a natural barrier to the spread of any given population. Thus, with habitats only spottily available, the evolutionary divergence that has resulted in localized species of *Mathewsia* is readily understandable.

One of the real difficulties in studying a group of species inhabiting areas that have been infrequently visited by botanists, is the paucity of available material. Furthermore, unlike some species of *Cremolobus* (Khanna and Rollins, 1965), the numbers of individuals in a given locality appear to be few and scattered. In some instances, only a single specimen of a given species has been found for study in all of the herbaria consulted. Under these circumstances, the bare essentials of the species are all that can be given and nothing can be said about their variation or distribution. The purpose of this paper is to present, as a first approximation, a taxonomic treatment of *Mathewsia* that will provide a sound basis for further research on the genus.

Mathewsia in Chile was briefly treated by Garaventa (1940). He recognized five species, *M. incana* Phil., *M. nivea* (Phil.) Schulz, *M. laciniata* Phil., *M. collina* Johnst., and *M. foliosa* H. & A. In this work a misinterpretation of *M. nivea* first made by Schulz (1928), in which the name was applied to plants with auriculate leaves and narrowly ovate fruits, was followed. It appears improbable that Schulz saw specimens of true *M. nivea*. At least, there were none cited. The material he called *M. nivea* is actually *M. auriculata* Phil. On the other hand, Garaventa was puzzled by the failure of accord between the short siliques, biseriate seeds and auriculate leaves, and the original description of *M. nivea*. It is doubtful whether he would have made the decision to place *M. auriculata* in the synonymy of *M. nivea* had he not had the precedent of Schulz to influence him. Actually, *M. nivea* and *M. auriculata* are wholly distinct species.

Mathewsia laciniata Phil. is a later name applied to the species named *M. biennis* by Turczaninow, who attributed it to Bridges. Details are given in the discussion of *M. biennis* below. In other respects, Garaventa's treatment of *Mathewsia* for Chile coincides with the results obtained in this study of the genus. There has been no other general treatment.

GENERIC RELATIONSHIPS

SCHULZ (1936) associated *Mathewsia* with genera such as *Erysimum*, *Thelypodium*, and *Hesperis* in the tribe *Hesperideae*. All of the genera he placed in the *Hesperideae* occur in areas outside of South America, *Mathewsia* being the single exception, and I cannot find among them any that could readily be considered phylogenetically close to *Mathewsia*. In using the specific name *matthioloides*, SCHLECHTENDAL (1857) obviously was reminded of the genus *Matthiola*, and, indeed, *Mathewsia matthioloides* does have a general resemblance to some species of *Matthiola*. If one were to follow this as a clue and associate these genera together, *Mathewsia* would fall in the tribe *Matthioleae* as it was constituted by Schulz (l.c.). However, it would again stand alone as the only South American genus in the tribe and it is equally difficult to find any genus within it whose species are obviously related to those of *Mathewsia*.

In considering the relationships of any genus, the geographical distribution matters only insofar as it helps in providing suggestions of reasonably related genera. For this reason, the geography of a genus should not be overemphasized. On the other hand, phytogeographical information should not be completely ignored and the first place to look is nearby, not continents away. Following this suggestion, I find a more plausibly related genus in *Schizopetalon* than in either the *Hesperideae* or the *Matthioleae*. If *Mathewsia* were to be associated with *Schizopetalon*, it would then be placed in *Schizopetaleae*. However, too little is known about the relationships of these and other possibly related genera of the *Cruciferae* to justify a revision of the present system of classification at this time. We can be confident that the species of *Mathewsia* make up a well marked genus that stands somewhat apart from other genera of the family.

GENERAL CHARACTERISTICS OF THE GENUS

Most of the species of *Mathewsia* are suffruticose at base or definitely woody. The low shrubby habit is well developed in such species as *M. incana*, which is appropriately described as a low bush. There is a very dense covering of leaves on nearly all specimens of *Mathewsia* I have seen (cf. Plate VI). This feature may not extend to *M. matthioloides* but our material of that species is too deficient to really determine the point.

The inflorescences eventually terminate every branch in *Mathewsia* and the branches may be leafy nearly to the lower flowers, as in *M. foliosa* (Plate II, Fig. 3) and *M. biennis* (Plate III), or there may be a distinct naked peduncle, as shown by *M. incana* (Plate VI, Fig. 2) and *M. densifolia* (Plate V). The racemes of flowers vary from short to elongate and may have a dense cluster of buds at the apex during development or only a few buds loosely arranged. The fully developed infructescence reflects this variation in the inflorescence and may have the siliques densely overlapping or somewhat separated (Compare Plate II, Fig. 1 and Plate VI, Fig. 2).

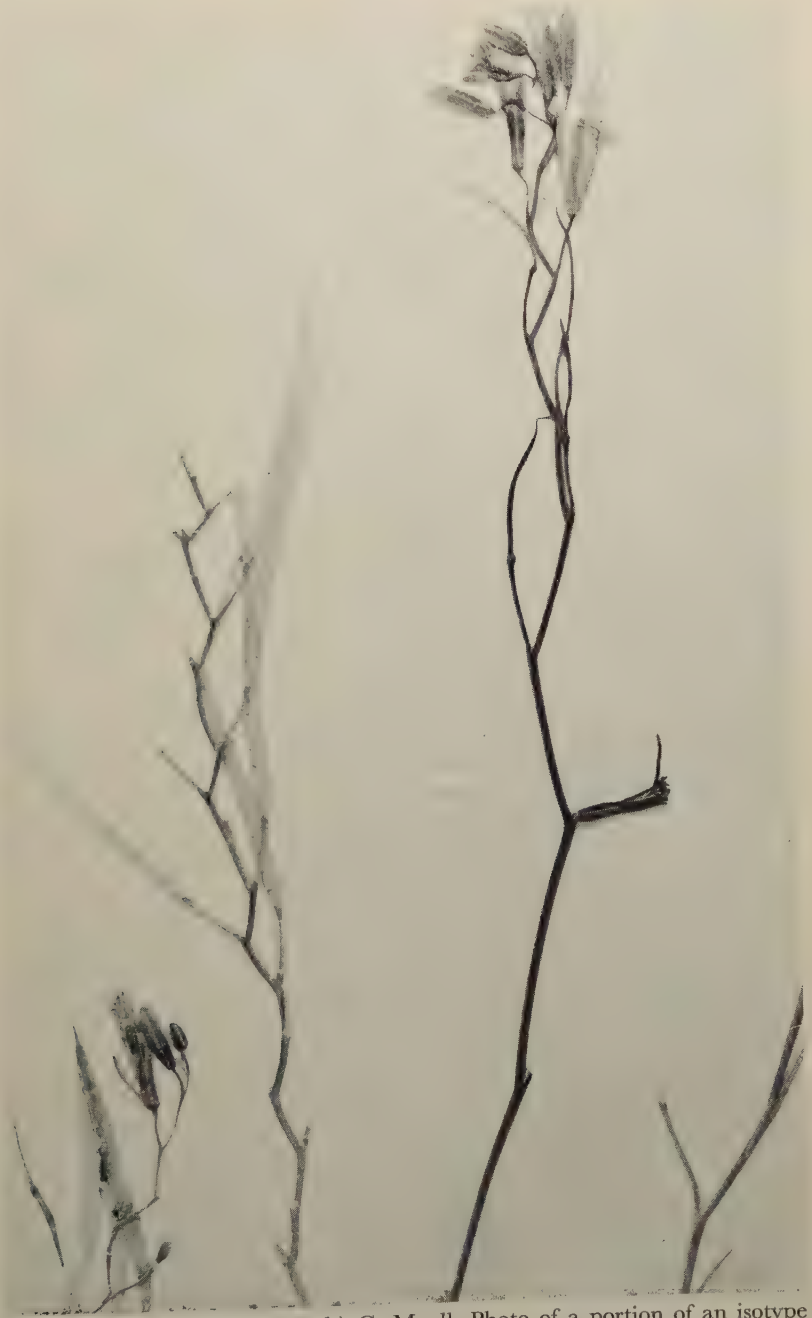
Mathewsia has relatively large flowers and the flower pattern is rather consistent throughout the genus. The calyx is cylindrical with the erect equal sepals closely appressed to form a tube. There is no evidence that the sepals open at all during anthesis. The petals are yellowish throughout the genus but not a clear yellow. There are brownish tones present and in the dried specimens the petals are quite dark. The petal claw is consistently very narrow, tapering to a width comparable to that of the filaments at the point of insertion on the receptacle. The petal blade is thick and is at its widest dimension near the middle rather than at the apex as in most genera of the *Cruciferae*. Throughout the genus, the stamens are nearly equal in length and the filaments slightly exceed the calyx but the anthers are scarcely exserted from the flower.

The four nectaries are erect, considerably elongated and discrete. In several of the species, the nectaries are sufficiently persistent to be present on the receptacle when the fruits are nearly mature. The valves of the silique are flattened parallel to the septum, and may possess a central nerve. In all but two species, *M. matthioloides* and *M. foliosa*, the siliques are very densely pubescent (cf. Plate V). The pubescence extends over the edge of the replum, at least above and below, and covers the style. It even extends to the interior of the valves in *M. biennis*. The plants of *Mathewsia* have a distinctive stigma. It is elongated, cylindrical and cap-like, without a noticeable indentation over the apex.

In all but two species, the seeds are well separated into two rows in each valve (Plate VI, Fig. 2). The separation is less definitive in *M. matthioloides* and scarcely so at all in *M. nivea*. The septum is thick and spongy in most of the species, tending to invest the seeds in deep depressions within it. The seeds are wingless and are much shorter than the width of the silique. The cotyledons are basically incumbent throughout the genus although in a few instances the radicle was not in a central position at the back of one of the cotyledons.

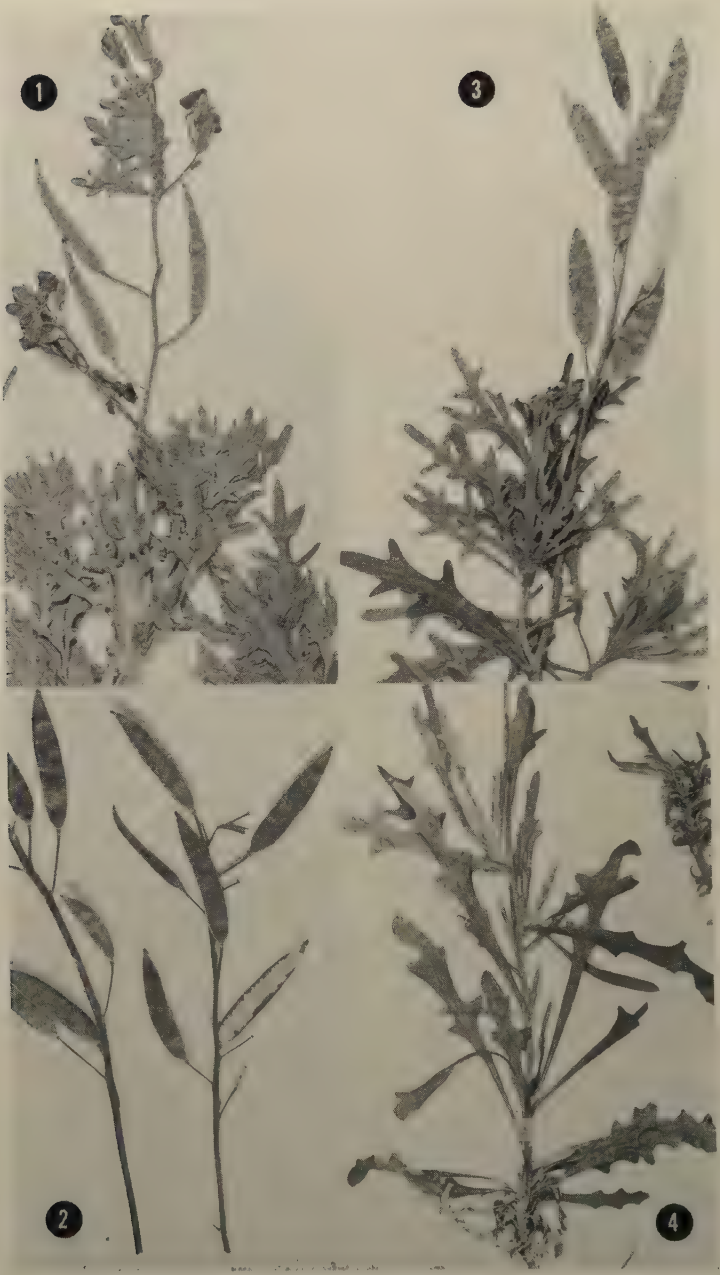
Aside from *M. matthioloides*, which is nearly glabrous, and *M. foliosa*, which is covered with minute trichomes, *Mathewsia* is characterized by the presence of a thick, dense indument. The trichomes are predominantly dendritic in form and are highly branched. The overall effect of the indument is to make the plants look tawny or off-white rather than green.

Type species: *Mathewsia foliosa* Hook. et Arn.



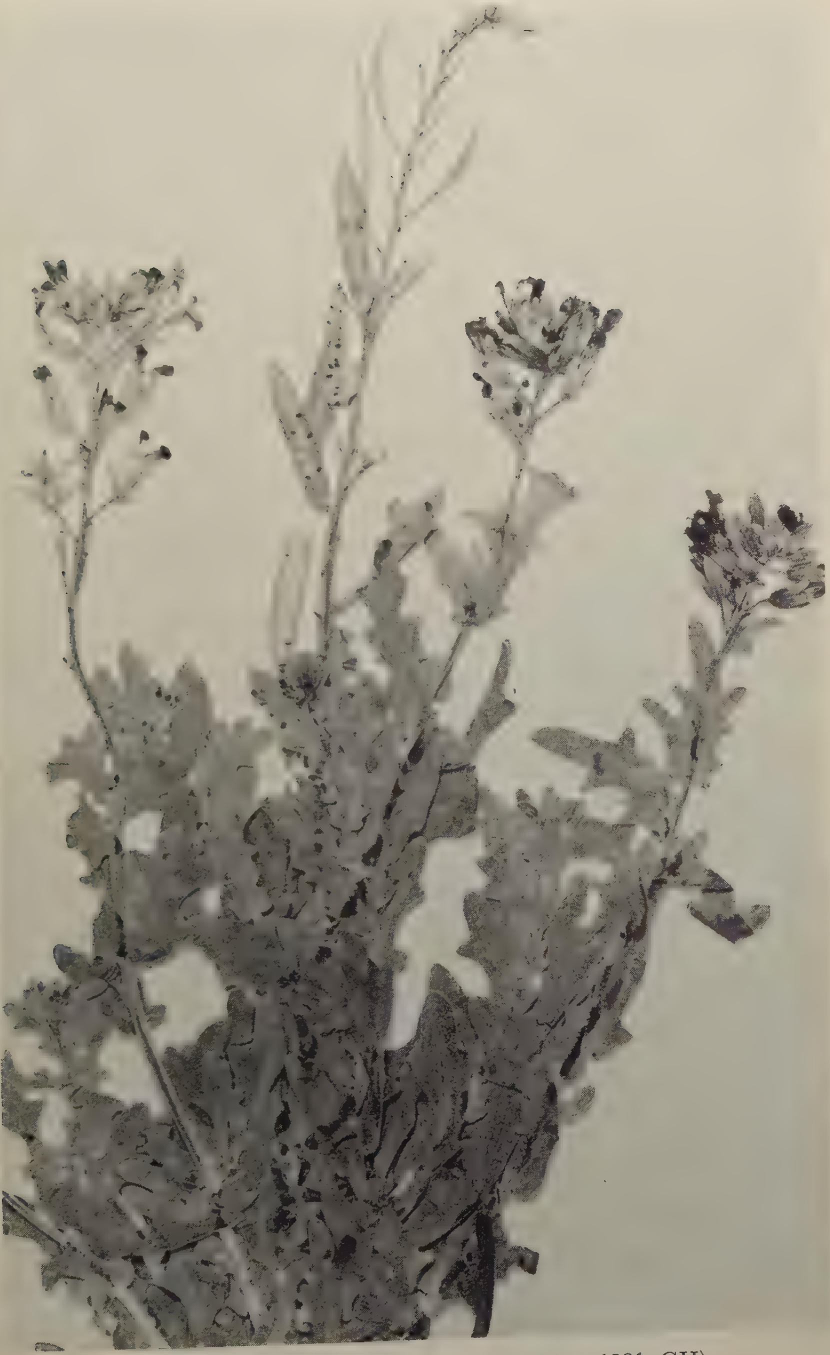
Mathewsia matthioloides (Schlechtd.) C. Muell. Photo of a portion of an isotype at Geneva. Note the excerted style in the lower flower at upper right of plate. The beak of the silique is evident at lower left.

Plate I



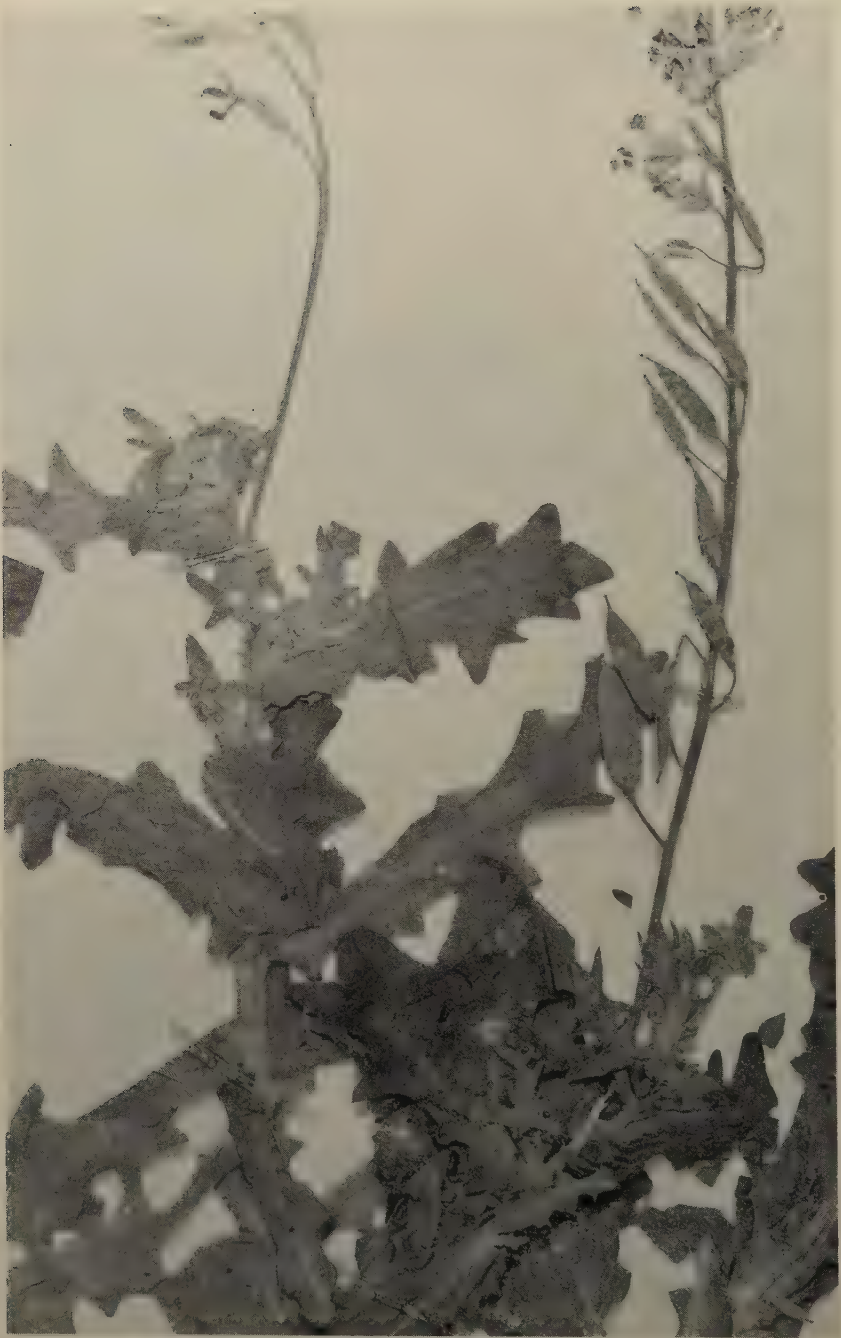
Figs. 1 & 2. *Mathewsia collina* Johnston (Johnston 3599, GH). Figs. 3 & 4. M. *foliosa* Hook. & Arn. (Fig. 3, Bertero 1296, G; Fig. 4, Bridges 479, GH).

Plate II



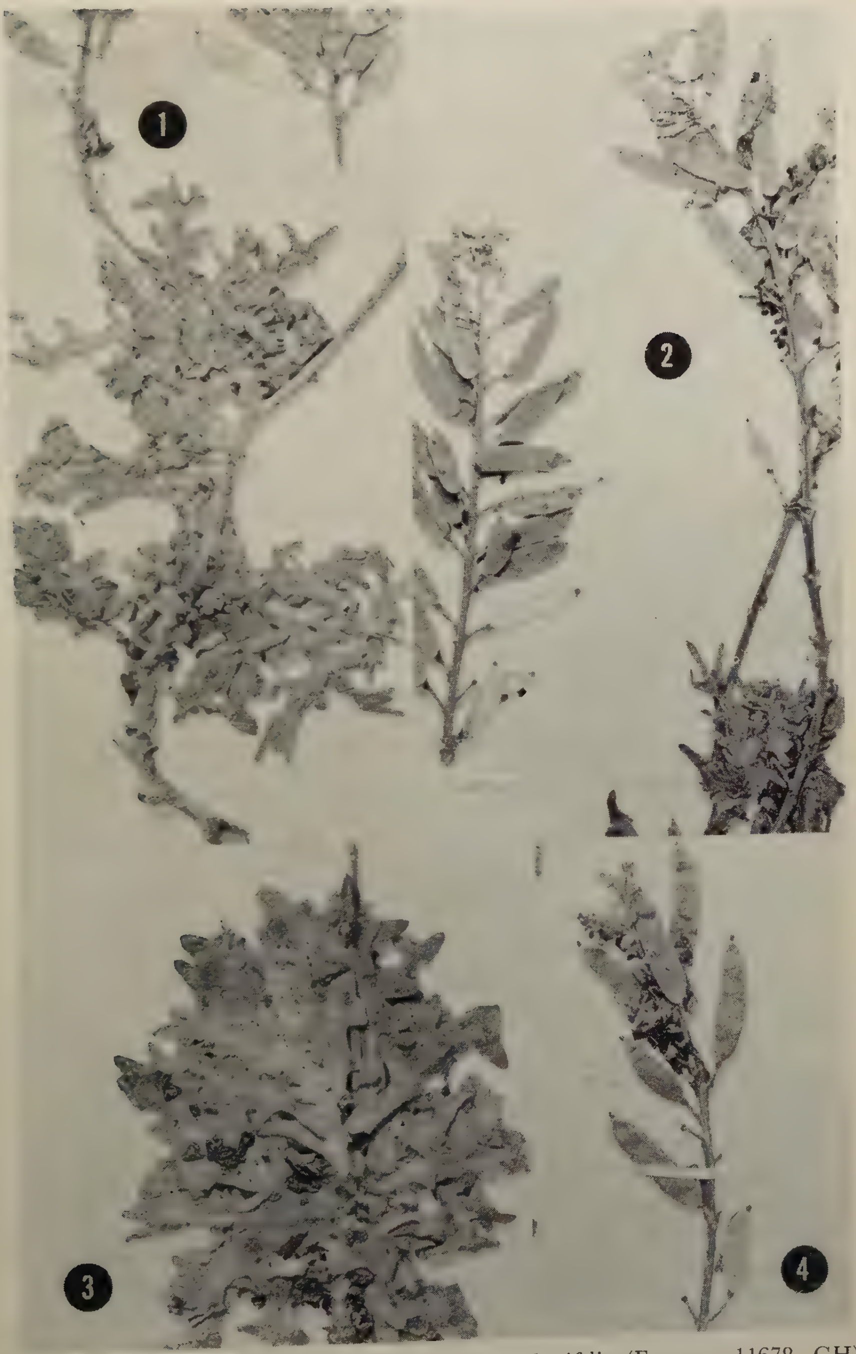
athewsia biennis Bridges ex Turcz. (Bridges 1281, GH).

Plate III



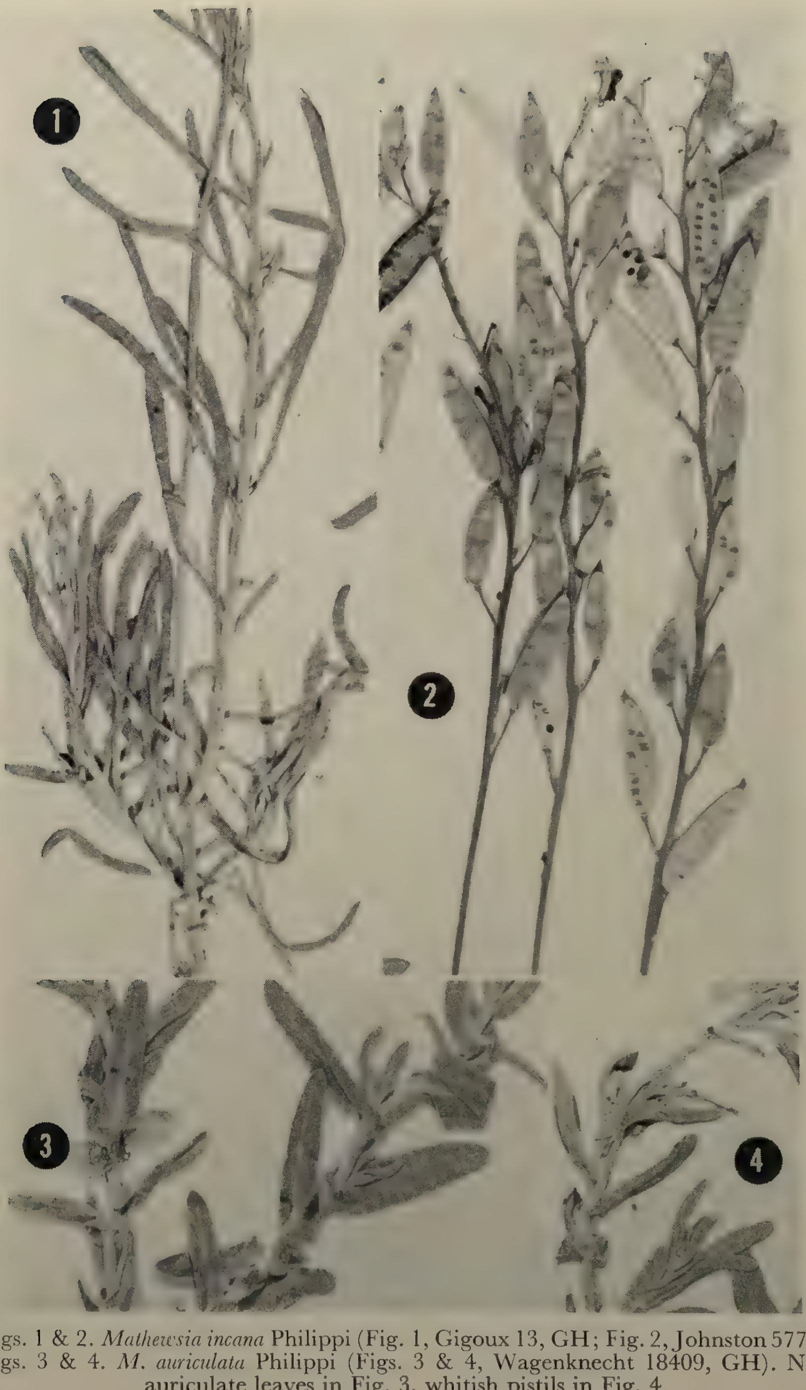
Mathewsia peruviana Schulz (Ferreyra 12493, GH).

Plate IV



Figs. 1 & 2. *Mathewsia densifolia* Rollins, var. *densifolia* (Ferreyra 11678, GH).
Figs. 3 & 4. *M. densifolia* var. *stylosa* Rollins (Vargas 8587, GH).

Plate V



Figs. 1 & 2. *Mathewsia incana* Philippi (Fig. 1, Gigoux 13, GH; Fig. 2, Johnston 5774). Figs. 3 & 4. *M. auriculata* Philippi (Figs. 3 & 4, Wagenknecht 18409, GH). Note auriculate leaves in Fig. 3, whitish pistils in Fig. 4.

Plate VI

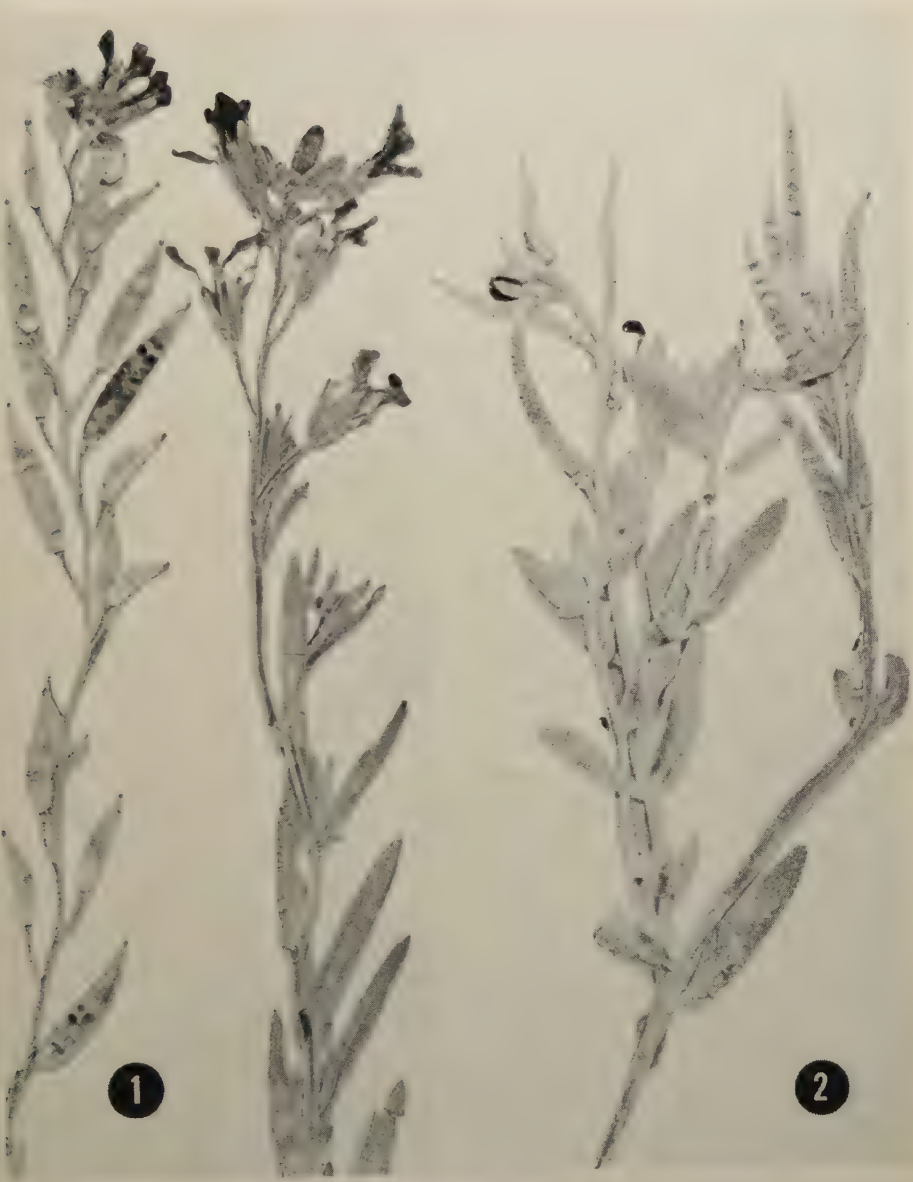


Fig. 1. *Mathewsia auriculata* Philippi (Geisse 47, NY). Fig. 2. *M. nivea* (Phil.) Schulz (Gigoux 1886, GH).

Plate VII

TAXONOMIC TREATMENT

Mathewsia Hook. & Arn., Hook. Bot. Misc. 3: 140. 1832.

Machaerophorus Schlechtd., Linnaea 28: 469. 1857.

KEY TO THE SPECIES

A. Leaves sinuate dentate to lobed, greenish to canescent.
    B. Siliques glabrous.
        C. Siliques narrowly linear, beaked toward apex, 4–6 cm long; pedicels glabrous. . . . . 1. *M. matthioloides*
        C. Siliques narrowly ovate, not beaked, 1.5–2 cm long; pedicels finely pubescent . . . . 2. *M. foliosa*
    B. Siliques densely pubescent.
        D. Lower flowers of raceme bracteate; valves pubescent on inner surface . . . . 3. *M. biennis*
        D. Lower flowers of raceme without bracts; valves glabrous on inner surface.
            E. Pedicels ascending, 6–10 mm long; leaves dorsiventral, strongly nerved below.
                F. Pubescence uniform on leaves and stems; trichomes short stalked, leaves lobed 4. *M. collina*
                F. Pubescence on stems and leaf veins much coarser than on leaf surfaces; trichomes long stalked; leaves mostly sinuate . . . . 5. *M. peruviana*
            E. Pedicels widely spreading, 3–5 mm long; leaves similar above and below, scarcely nerved . . . . 6. *M. densifolia*
A. Leaves entire, canescent.
    G. Leaves narrowly linear; seeds nearly round, reticulate; infructescences borne on naked peduncles . . . . 7. *M. incana*
    G. Leaves oblong; seeds definitely longer than broad, smooth; infructescences borne on leafy branches.
        H. Leaves auriculate; siliques narrowly ovate; seeds in two separated rows in each valve of the silique 8. *M. auriculata*
        H. Leaves non-auriculate; siliques linear, seeds in a single row in each valve of the silique . . . . . 9. *M. nivea*

1. **Mathewsia matthioloides** (Schlechtd.) C. Muell.

Walp. Ann. Bot. Syst. 7: 144. 1868.

Machaerophorus matthioloides Schlechtd., Linnaea 28: 469-471. 1857.

Plants nearly glabrous throughout; cauline leaves linearly pinnatifid; rachis of infructescence markedly flexuose; pedicels straight, divaricate, 1–2 cm long; flowers erect, style becoming exserted as flower matures; sepals linear-oblong, ca. 1.5 cm long, glabrous; petals unguiculate, up to 2.5 cm long, claw long, narrow and gradually expanded to a thickened blade; siliques divaricately ascending to erect, narrowly linear, flattened, glabrous, 4–6 cm long, 2–2.5 mm wide, tapering above into a definite beak that is up to 1 cm long; styles 2–3 mm long; stigma globular to cylindrical; septum spongy, much involuted and nearly investing the seeds; funiculi stout, ca. 1 mm long, seeds not filling silique width, more or less in two rows in each valve, wingless, oblong and plump, ca. 1.5 cm long, less than 1 mm wide; cotyledons incumbent.

Peru: rupestribus Cordillerae de Tuno-Maio, M. 1854, "W. Lechler pl. Peruvianae". Ed. R. F. Hohenacker. 1702 (G, isotype).

There is no doubt about the correctness of placing this species in the genus *Mathewsia*. It not only has many of the characteristics exhibited by species of *Mathewsia* but there are no easily observable features that would justify its being withdrawn from the genus. This is true even though the species has much larger flowers, narrower and longer fruits than any other known species and a distinctive narrowing silique apex that forms a beak below the style. The upper portions of the stems, particularly the rachises of the inflorescences, are markedly flexuose. The flowers and fruits are borne on stiff pedicels that arise on the outside of each bend of the rachis (Plate I).

Apparently *M. matthioloides* is rare because only the type collection is known. The isotype from Geneva that I have studied consists of only the upper portion of the plant. The oldest flower of the inflorescence on one branch has the stigma considerably exserted. This suggests the possibility of protandry in the species.

2. **Mathewsia foliosa** Hook. & Arn.

Hook. Bot. Misc. 3: 140–141, tab. XCVI. 1832.

Plants suffrutescent, 2–5 dm high, usually with an elongated foot below the active leaves; leaves densely overlapping on the stems, narrowed to the base, deeply lobed to nearly pectinate, densely pubescent with minute dendritic trichomes, margins rolled toward under side; sepals erect, densely pubescent, 5–8 mm long; petals 1.5–2 cm long, claw exceeding sepals in length, blade narrowing toward apex, yellowish; pedicels slender, straight, ascending, 1–1.5 cm long; valves veiny, central nerve prominent; style 1–1.5 mm long; siliques flattened, narrowly oblong, 1.5–3 cm long, 5–7 mm wide; seeds oblong, plump, wingless, in two separated rows in each valve; cotyledons incumbent.

Chile: without locality, 1828, *Peppig 145* (G); 1829, *John Style* (G); *Bridges*, [Cuming] (G); *Bertero* (GH); *M. Guillemin* (GH). Prov. Valparaiso: Cliffs at Playa Aucha, Valparaiso, *Bridges 479* (GH, isotype; photo of type at GL); Valparaiso, 1835, *Dr. Gay* (G); Valparaiso. 1856–57, *Ph. Germain* (G); Valparaiso, Sept., 1830, *M. Bertero 1296* (G, GH, NY); Valparaiso, July 24, 1931, *C. Junge* (BAB, AA); Valparaiso, July 15, 1931, *F. Jaffuel 1753* (GH); Quintero, Nov., 1923, *Werdermann 27* (BAB, F, G, GH, UC, US); Quintero, Sept., 1963, *O. Zöllner 319* (GH). Prov. Coquimbo: Coquimbo, July-Aug., 1856, *W. H. Harvey* (GH); Viña del Mar, Aug. 27, 1933, *D. H. Behn* (UC); Loma Frai Jorge, Aug. 17, 1917, *C. & O. Skottsberg 853* (F, NY); Zapallar, Sept. 20, 1923, *D. H. Behn* (F).

The very dense, minute, highly branched trichomes covering the leaves, stems, pedicels and sepals in *M. foliosa* do not produce a canescent appearance as in such species as *M. nivea* and *M. incana.* The glabrous siliques are also in striking contrast to the indument covered parts of the plant. In this species, as in others of the genus, the seeds are small compared to the total width of the siliques and basically form two separate rows. Here they tend to lie near the replum margin, leaving a relatively large unoccupied space toward the center of the silique. The septum of the silique is a dense opaque structure but without the spongy convoluted characteristic found in the septum of *M. matthioloides.*

All of the specimens referable to *M. foliosa* without question, have leaves that gradually taper to a narrow base without auricles (Plate II, Fig. 4). However, there is a specimen collected at Valparaiso without flowers or fruit and now deposited in the Museum of the University of La Plata, that seems to belong to *M. foliosa* but the leaves are auriculate at the base. If the leaf variation ranges as widely as this specimen would suggest, the variation pattern is somewhat broader than I have indicated. Actually, it is probable that the fragment in question represents an entirely different species.

Hooker's illustration of *Mathewsia foliosa* provides a good indication of the habit of this species. There must be a rather extensive woody "foot" present on most plants but it is difficult to be sure on this point because the lower woody portion of the plant is usually not included as part of the specimen. As far as I can determine, the plants are not extensively branched. Usually there are two to four branches arising at points considerably above the base.

3. **Mathewsia biennis** Bridges ex Turcz.

Bull. Soc. Nat. Mosc. 36: 550. 1863.

M. laciniata Philippi, Anal. Univ. Chile, 81: 194. 1892.

Perennial with a short suffruticose foot, branched from near the base; stems whitish pubescent, leafy, 2–3 dm high, leaves mostly sessile, auriculate, deeply dentate to irregularly lobed, oblong in outline, densely pubescent with highly branched trichomes, 2–4 cm long, 1–1.5 cm broad, lowermost leaves sometimes with a broad petiole and no auricles; lower flowers often bracteate; sepals erect, pubescent, narrowly oblong, 7–9 mm long, 1.5–2 mm wide; petals unguiculate, yellowish, 13–16 mm long, 2–3 mm wide, blade ovate, blunt at apex, claw very narrow; stamens equal or nearly so, anthers ca. 3 mm long; pedicels straight, divaricately ascending, whitish pubescent, 4–6 mm long; siliques ascending, flattened, whitish pubescent, narrowly oblong, 1.5–2.5 cm long, 3–4 mm wide, valves pubescent on inner surface, replum pubescent on outer margin; stigma conical, elongated; style less than 0.5 mm long; seeds in two distinct rows (Plate III), oblong, plump, reticulate, ca. 15 mm long, just above 1 mm wide, not mucilaginous; cotyledons incumbent.

Chile: without locality or other data, *Fielding* (GH); hills near Loz Pozos, between Huasco and Copiapo, Prov. Coquimbo, 1844, *Bridges 1280* (G, GH, isotypes); Desert of Atacama, 1885-87, *William Geisse 158* (NY, isotype of *M. laciniata*).

A specimen of *M. biennis* at Kew has the following label data: "Hexaptera pinnatifida 4 1–2 ft Dec. 6 Jan. 2 Mts. near snow E & N side of the Andes, Bridges 1118". These data appear to be erroneous because the species does not grow "near snow" or East and North of the Andes. The specimen is so similar to the material of Bridges 1280, I am inclined to believe it is a part of that collection that has somehow gotten wrong label data.

The original description of *M. biennis* was given by TURCZANINOW (1854) without a specific epithet being mentioned. Later (1863) he supplied the name *M. biennis* for the species, attributing it to Bridges. Turczaninow's assumption that the species is a biennial is almost certainly based upon the appearance of the specimens and not upon a knowledge of the growth cycle of the species. The specimens do look somewhat like a biennial but I believe the hard woody foot is more indicative of a perennial species. I am familiar with many desert species that flower the first year and if collected as specimens at that time would then be taken for annuals or at most biennials. However, these same plants continue to live and become increasingly shrubby over a period of years.

It is quite probable that the material of this species I have studied is all traceable to two collections, one by Bridges and the other by Geisse. The Fielding specimen certainly looks enough like Bridges 1280 to be part of the same collection.

4. **Mathewsia collina** Johnston

Contrib. Gray Herb. 85: 148. 1929.

Small fruticose bush with semi-decumbent outer branches, 3–5 dm high; stems leafy, whitish below with a fine, dense pubescence, greenish above; leaves sessile, dentate to pinnately lobed, narrowly oblong in outline, with a strong single nerve, 4–6 cm long, 1–2 cm wide, densely pubescent with minute highly branched trichomes, somewhat greenish in appearance, lowermost subauriculate, upper auriculate; inflorescence pedunculate, peduncle 3–6 cm long; sepals erect, narrowly oblong, densely pubescent, 6–8 mm long, 2–3 mm wide; petals cream-colored, 10–14 mm long, 3–4 mm wide, unguiculate, spatulate, broadest about middle of blade and narrowing to a blunt apex, claw slender; single stamens barely shorter than paired stamens; anthers acute at apex, ca. 3 mm long; pedicels 6–10 mm long, slender, straight, divaricately ascending, usually at about a 45 degree angle, densely pubescent, slightly expanded at summit; 4 conspicuous triangular nectar glands persistent on receptacle; siliques flattened, lanceolate, rounded below, gradually tapering above, 2–3 cm long, 3–4 mm wide, densely pubescent with minute highly branched trichomes; valves covering replum except at base and apex, glabrous on interior; replum pubescent at base and apex; style less than 1 mm long, densely pubescent; stigma expanded, nearly entire, immature seeds in two distinct rows, plump, very slightly longer than broad, reticulate, ca. 1.5 mm long, emitting a mucilaginous coating when wet; disposition of cotyledons with respect to radicle not determinable.

Chile: infrequent on talus slope, steep hillside, ca. 6 km north of Port and opposite Caleta Duendes, Tocopilla, Dept. Tocopilla, Prov. Antofagasta, Oct. 18, 1925, *I. M. Johnston 3599* (GH, type); Tocopilla, Oct., 1932, *Felix Jaffuel 2580* (GH).

Johnston correctly placed this species near *M. laciniata* [= *M. biennis*] and *M. foliosa.* In many ways it is intermediate between them in its characteristics (Plate II, Figs. 1 & 2). For example, the pubescence of *M. collina* is much finer and less matted than in *M. biennis* and does not produce the white tomentose appearance characteristic of *M. biennis.* On the other hand, the trichomes of *M. collina* are not as minute as those covering the leaves and stems of *M. foliosa* and the appearance of plants of the latter species is greener than in *M. collina.* In *M. foliosa* particularly, the covering of trichomes is relatively inconspicuous to the naked eye. The three species mentioned, although related, are amply distinct from one another and can be readily separated, as shown by the characters stressed in the key.

Unfortunately, I have not had mature seeds available for dissection and could not determine the exact position of the cotyledons with respect to the radicle. The shape of the seed suggests that the cotyledons might be accumbent. If that is so, *M. collina* differs from other species of the genus in this respect.

5. **Mathewsia peruviana** O. E. Schulz

Notizbl. Bot. Gart. Berl. 10: 562. 1929.

Plants suffruticose at base, pubescent throughout with mixtures of highly branched dendritic and sessile trichomes, leafy below the inflorescences, whitish tomentose, up to 5 or 6 dm high; leaves sinuate dentate to irregularly lobed, narrowly obovate to oblong in outline, sessile, upper auriculate and amplexicaule, lower subauriculate to auriculate, 4–12 cm long, 1–4 cm wide, dorsiventral, densely pubescent with minute highly branched trichomes on upper surface, often with larger stalked dendritic trichomes sparsely scattered over the surface and abundant along the mid-vein, lower surface pubescent with predominantly stalked branching trichomes; inflorescences 1–3 dm long, pedunculate, peduncle ca. 5 cm long, sepals narrowly oblong, acute, densely pubescent, 6–8 mm long, ca. 2 mm wide; petals unguiculate, yellowish, 14–18 mm long, ca. 4 mm wide, blade ovate, abruptly narrowed to a slender claw, tapered to a blunt apex; stamens equal, filaments equalling sepals at full anthesis, elongating as the flower ages, nectar glands persistent, lingulate; anthers ca. 3 mm long; pedicels divaricately ascending, straight or slightly incurved, 6–9 mm long; sometimes secund; siliques densely pubescent, flattened, narrowly ovate, rounded below, tapered above, 2–3 cm long, 4–5 mm wide, replum pubescent on outer margin; styles pubescent, 1–2 mm long; stigma conical, nearly 1 mm long; seeds in two distinct rows, immature in the available material (Plate 4).

Peru, Dept. Arequipa, Prov. Caravelí: Lomas de Atico, Loma llamada del Taro, 1863, *Raimondi 11632* (Photo of type, F, GH); Lomas de Atico, entre chala y Camaná, Oct. 3, 1957, *Ramon Ferreyra 12493* (GH); same locality, Oct. 10, 1956, *Ferreyra 11946* (GH).

Raimondi gave the flower color as white on the label of the type specimen but Schulz evidently felt this might be an inaccuracy. In the original description, he was careful to attribute the designation of white flower color to Raimondi and, at the same time, indicated that in the dried specimens the color was obscurely brown. In both collections Ferreyra made, he noted the flower color to be "amarillentas" or yellowish. This fits the pattern for the genus and I am reasonably certain *M. peruviana* has yellowish flowers.

The lack of adequate material of *M. peruviana* leaves a lot to be desired in the way of information. Practically nothing about the range of variation can be discerned from the two specimens at hand because, although they both fit the general description of *M. peruviana*, they differ from each other in important ways and may possibly represent distinct taxa.

6. **Mathewsia densifolia** Rollins, sp. nov.

Plants herbaceous above and with a woody foot below, 1–2 dm high, densely covered throughout with a whitish to tawny indument of highly branched and matted trichomes; leaves densely clustered above the naked woody foot, sessile or short-petiolate, non-auriculate, oblong in outline, pinnately lobed, 2–4 cm long, ca. 1 cm wide, lobes linear-oblong to broader; inflorescence pedunculate; sepals erect, narrowly oblong, 5–6 mm long, 1.5–2 mm wide, densely pubescent; petals yellowish, unguiculate, narrowly spatulate with a narrow claw and attenuate to a narrow apex, widest above middle, 12–15 mm long, 2.5–3 mm wide; stamens nearly equal, pedicels straight, divaricately ascending to more widely spreading, 3–5 mm long; conspicuous, persistent, lanceolate nectar glands present on receptacle; siliques sessile, divaricate, flattened, oblong, rounded above and below, densely pubescent, ca. 1.5 cm long, 3.5–4.5 wide; replum covered by valves and glabrous except at apex and base where trichomes are present; stigma sessile or on a short style less than 1 mm long, conical, ca. 1 mm long; septum convoluted, dense, nearly enveloping seeds; seeds in two distinct rows, plump, longer than broad, ca. 2 mm long, ca. 1.5 mm broad, reticulate, conspicuously mucilaginous; cotyledons incumbent to obliquely incumbent.

Planta suffruticosa incana 1–2 dm alta; foliis oblongis pinnatifidis cano-pubescentibus sessilibus non-auriculatis 2–4 cm longis, ca. 1 cm latis; sepalis erectis anguste oblongis pubescentibus 5–6 mm longis, 1.5–2 mm latis; petalis unguiculatis fulveis anguste spathulatis superne attenuatis 12–15 mm longis, 2.5–3 mm latis; infructescentiis pedunculatis; pedicellis divaricatis rectis pubescentibus 3–5 mm longis; siliquiis oblongis obtusis compressis cano-pubescentibus ca. 1.5 cm longis, 3.5–4.5 mm latis; seminibus oblongis emarginatis brunneis reticulatis ca. 2 mm longis, ca. 1.5 mm latis; cotyledonibus incumbentibus.

Key to the Varieties

Stigma sessile; leaf-segments narrowing to an acute apex . . . . 6a. var. *densifolia*
Stigma raised on a definite style; leaf-segments obtuse and broader . . . . 6b. var. *stylosa*

6a. **M. densifolia**, var. **densifolia**

Type in the Gray Herbarium collected at Lomas de Tambo, Prov. Islay, Dept. Arequipa, Peru, Dec. 2, 1955, *Ramon Ferreyra 11678.*

6b. **M. densifolia** var. **stylosa** Rollins, var. nov.

Planta suffruticosa; foliis obtusis, stylis plus minusve 1 mm longis.

Type in the Gray Herbarium collected at Ilo, Lomas de Mostacilla, Prov. Maguegua, Dept. Maguegua, Peru, Nov., 1949, *C. Vargas C. 8587.*

Mathewsia densifolia has the silique shape and disposition in the infructescence (Plate V) characteristically found in *M. incana* but the leaves are not at all linear and entire but are more like those of *M. linearifolia.* From an examination of a photograph of the type of *M. peruviana,* I was nearly ready to conclude that the specimens here described should be referred to *M. peruviana.* However, the receipt from Professor Ramon Ferreyra of good specimens from the type locality of *M. peruviana* made it abundantly clear that three, not two, very distinct species of *Mathewsia* occur in Peru, *M. matthioloides, M. peruviana* and *M. densifolia.*

It is risky to set up two varieties of a species on the basis of only two collections but such a treatment represents my best estimate of the taxa present. Although no real evidence on population variation is available, the fact that the specimens from two different locations show two differences that may be presumed to be correlated, strongly suggests the presence of two minor taxa in these separated lomas.

According to the collector's notes, *M. densifolia* grows below 700 meters in rocky or gravelly places.

7. **Mathewsia incana** Philippi

Fl. Atacama 8. 1860.

Plants shrubby and considerably branched above the base, 3–10 dm high, up to 8 dm in diameter, branches erect, mostly terminated by inflorescences; leaves densely covering the actively growing parts of the bush, linear, entire, narrowed to base, non-auriculate, 2–5 cm long, 2–4 mm wide, whitish from a dense thick covering of highly branched trichomes; buds oblong; sepals remaining erect during anthesis, densely pubescent, 5–7 mm long; petals linear with a very narrow claw, yellowish, 10–14 mm long; stamens exceeding the calyx, all six filaments nearly equal in length; infructescence narrow, racemose, elevated on a naked peduncle, pedicels straight, divaricately ascending, 5–10 mm long, scarcely expanded at summit; siliques narrowly ovate to narrowly oblong, flattened, erect to slightly divergent, 1.5–2.5 cm long, 3.5–5 mm wide, valves densely pubescent, 1-nerved below, replum pubescent on outer margin, septum dense, spongy, style pubescent, 0.5–1 mm long, stigma enlarged and elongated, entire; seeds wingless, plump, only very slightly longer than broad, ca. 1 mm long, in two well separated rows; cotyledons incumbent (Plate VI, Figs. 1 & 2).

Chile: Desert of Atacama, Sept.-Oct. 1890, *T. Morong 1129* (NY, US); Carrizal Bajo, *R. A. Philippi* (CORD); western part Prov. Atacama, 1922, *E. E. Gigoux 13* (GH); Quebrada del Leon, north of Caldera, Copiapo, Atacama, Oct. 20, 1938, *Worth and Morrison 16148* (UC); same locality, Nov., 1924, *Werdermann 442* (BAB, GH, NY, UC, US); vicinity of Aguada Grande, near Antofagasta, Atacama provincial boundary, Dec. 16–18, 1925, *Johnston 5774* (GH); region about Aguada Cachina, ca. 6 km inland from Caleta Esmeralda, Taltal, Antofagasta, Dec. 14–15, 1925, *Johnston 5748* (F, GH); El Rincon, just north of Paposo, Taltal, Antofagasta, Dec. 7, 1925, *Johnston 5516* (GH).

Mathewsia incana is found in dry areas near the coast of northern Chile. It is definitely of shrubby growth, and appears to vary considerably in compactness and height. One report indicates the plants may attain a height of as much as 2 meters. However, many plants are only a few decimeters tall. Active leaves tend to be concentrated near the ends of branches and there are extensive areas on the older parts of the plants that are essentially devoid of leaves or sometimes possess only dead leaf-remnants.

The growing parts of *M. incana* are very densely and thickly clothed with white highly branched trichomes. JOHNSTON (1929) in an apparently contradictory statement says that the siliques of the type and his own collection from Aguada Grande are glabrate or inconspicuously pubescent. However, I have carefully studied his collection (no. 5774) and find the siliques densely pubescent with minute trichomes but with mature valves that appear non-pubescent to the naked eye. I have not seen the type of *M. incana*. However, Johnston compared one of his own specimens with the Philippi type in Santiago and annotated the material as being the equivalent of the type. Johnston's specimen was collected in the type locality. There is no problem in fixing the proper application of the name.

The name *Mathewsia angustifolia* Philippi has appeared in synonymy under *M. incana* in at least two places but I cannot find evidence that it was properly published. It appears to be merely a name without any status and need not be taken into account in any way.

8. **Mathewsia auriculata** Philippi

Anal. Univ. Chile 81: 193. 1892.

Small shrub or woody-based perennial, densely clothed with whitish or tawny highly branched trichomes, branched near base and above, 2–4 dm high; leaves entire, sessile and auriculate, densely and thickly pubescent, oblong, obtuse, 1.5–4 cm long, 3–5 mm wide, overlapping along the active portions of the stems; inflorescences 5–10-flowered on leafy branches; sepals oblong, densely pubescent, erect at anthesis, 6–8 mm long; petals yellowish, linear-spatulate, 12–15 mm long, claw very narrow; filaments of all stamens nearly equal in length, anthers narrowly oblong, lobes separated at base; pedicels straight, erect to divaricate, 5–10 mm long, scarcely expanded at summit; siliques narrowly ovate, flat, tapering to rounded at apex, densely pubescent including replum margin and style, 1.5–4 cm long, 4–6 mm wide; style 0.5–1.5 mm long; stigma enlarged, cylindrical; septum dense, spongy, nearly embedding seeds; seeds oblong, wingless, plump, ca. 1.5 mm long, 1 mm wide, in two separated rows in the silique; cotyledons incumbent (Plate VI, Figs. 3 & 4; Plate VII, Fig. 1).

Chile: Desert of Atacama, *R. A. Philippi* (CORD, US, isotypes; F. GH, photo of specimen at B); 1885–7 *William Giesse* (NY); Huasco, Atacama, *R. A. Philippi* (CORD, US); Quebrada Canchas, Copiapo, Atacama, Sept., 1924, *Werdermann 422* (GH, UC); Cuesta Monte Grande, 20 km on road Rivadavia to Pisco Elqui, Elqui, Coquimbo, Aug. 5, 1939, *Wagenknecht 18409* (F. GH, UC).

The typification of *M. auriculata* has presented something of a problem because no Philippi specimen bearing the locality "Carrizal Bajo", as given in the original publication of the name, could be located. Apparently Muñoz (1960) did not locate the type at the time he listed the specimens with which Philippi names are to be associated and this raises the question as to whether the type is preserved at the Museo Nacional in Santiago. However, the application of the name is quite certain on the basis of two sheets labeled "Mathewsia auriculata Ph. desertum Atacama" in the handwriting of Philippi. These sheets are on loan from the Museo Botánico at Córdoba and the U.S. National Herbarium. It is reasonably certain these are isotypes and I have so labeled them.

Philippi also collected and distributed specimens of this species with the label name *M. subauriculata*. These were obtained at Huasco. I cannot find that Philippi ever published the epithet *subauriculata* but it was picked up, apparently from the labeled specimen at Berlin, by Gilg and Muschler (1909). They gave the name in a new combination as a variety of *M. auriculata*. However, no description was supplied and, since the name had no published status previously, it is a *nomen nudum*. These Philippi specimens do differ from the type material of *M. auriculata* in minor ways, but considered in the frame of the total known variation of *M. auriculata*, they scarcely represent a distinctive formal taxon of any rank.

Mathewsia auriculata is most closely related to *M. nivea* and *M. incana*. From *M. nivea*, the species differs in having the seeds in two well separated rows in the silique instead of the nearly single row characteristic of *M. nivea*, by having a narrowly ovate broad silique in contrast to a linear much narrower one as in *M. nivea*, and by having definitely auriculate leaves instead of non-auriculate leaves. Actually, the silique-shape is somewhat similar in *M. auriculata* and *M. incana*, but here the leaf-shape is widely different. In *M. incana*, the leaves are linear and non-auriculate, whereas in *M. auriculata*, they are oblong and auriculate. These two species can be readily distinguished from the seeds alone. The seeds of *M. incana* are nearly round or only very slightly elongated and the surface is conspicuously reticulate, while those of *M. auriculata* are smooth-surfaced, and at least one and one-half times longer than broad. Of course, it is difficult to be certain about growth habit unless one has had field experience with the species, but from what I can learn from label data and published sources, *M. incana* tends to be a relatively tall, somewhat sprawly shrub, often growing to a meter or more in height, while *M. auriculata* is a low subshrub, woody at the base only, and usually a few decimeters high.

9. **Mathewsia nivea** (Phil.) O. E. Schulz

Notizbl. 10: 465. 1928. Based on *Sisymbrium niveum* Phil.

Fl. Atac. 8. tab. I, fig. A 1–5. 1860.

Hesperis nivea (Phil.) O. Ktze., Revis. Gen. Pl. pt. 2: 935. 1891.

Plant suffruticose at base, fully clothed with a very dense whitish to tawny indument, trichomes of two types; dendritic type with a central axis fewer in number and exceeding in length a more extensive, compact and more highly branched type; leaves entire, sessile, rounded at base but not auriculate, 1.5–2.5 cm long, 4–8 mm broad; stems branched above; sepals erect, non-saccate, 8–10 mm long; petals erect, linear to linear-spatulate, 15–18 mm long; pedicels thick, erect, 3–5 mm long, summit markedly expanded, nectary prominent; siliques erect to slightly divaricate, crowded, linear-oblong, 2–3 cm long, 2.5–3 mm wide; septum dense but not spongy; style densely pubescent, less than 1 mm long; stigma bilobed; seeds in a single row, oblong, ca. 2 mm long, wingless; cotyledons incumbent, unequal, radicle exceeding the cotyledons (Plate VII, Fig. 2).

Chile: Prov. Atacama. Quebrada de Doña Ines Chica, Dept. Chanaral, Jan. 1886, *E. E. Gigoux* (GH); gulch below hospital, vicinity of Portrerillo, Oct. 22, 1925, *Johnston 2666* (GH); below Mina Maricunga, in Quebrada del Mono, Dept. Copiapo, Nov. 3–4, 1925, *Johnston 4847* (GH).

It is clear from Philippi's original description and drawing of *Sisymbrium niveum* that this species does belong to the genus *Mathewsia*, a disposition now well established. One point stressed by Philippi but ignored or overlooked by later authors is that the seeds are disposed in a single row in the silique. In many crucifers, there is variation as to seed disposition and this feature needs to be handled with caution. In this case, the single-rowed seeds do not provide a mandate to place *M. nivea* in *Sisymbrium* as Philippi believed, but, on the other hand, this character does aid in establishing the distinctness from closely related species having two rows of seeds.

Schulz (1928) attributed material (*Werdermann 422*) to *M. nivea* that is actually *M. auriculata*. From his listing of *M. auriculata* as a synonym in Die Natürlichen Pflanzenfamilien (1936), I assume he considered both names to apply to the same species. However, I do not agree that this is the case

This species grows in the mountains of northern Chile at altitudes of 2500 to 3500 meters. The few specimens I have studied certainly do not indicate the total geographic range. According to Johnston's notes, the plants grow in loose soils on hillsides or at the base of talus slopes and are definitely woody at the base where the main branches of the plants arise. All of the principal branches and most of the subsidiary branches above are terminated by a compact racemose inflorescence that is less than a decimeter long. In habit and general appearance *M. nivea* is somewhat like the North American *Nerisyrenia camporum*.

Flowering material of *M. nivea* is most likely to be confused with *M. auriculata*. However, the base of the leaf of *M. nivea* is definitely not auriculate, even though in some plants the leaf scarcely narrows at the point of attachment to the stem. In fruit, there is no problem of distinguishing between these two species, because in *M. nivea*, the silique is linear and the seeds are in one row, whereas in *M. auriculata*, the silique is narrowly ovate and the seeds are in two well separated rows.

SPECIES EXCLUDED OR NAMES OF UNCERTAIN APPLICATION

M. boliviana Gilg and Muschl., Engl. Bot. Jahrb. 42: 464. 1909 = *Kardamoglyphos nana* Schlechtd. 1856 = **Rorippa nana** (Schlechtd.) Macbr.

M. diffusa Rusby, Bull. N. Y. Bot. Gard. 4: 322. 1907 = *Kardamoglyphos nana* Schlechtd. = **Rorippa nana** (Schlechtd.) Macbr.

Both *M. boliviana* and *M. diffusa* were based on the same collection, Miguel Bang, no. 1967, from Bolivia. I have seen five sheets of this number at F, NY, US.

M. linearifolia Turcz., Bull. Soc. Nat. Mosc. 36: 550. 1863. This name is based on a collection of Bridges, from Coquimbo, Chile, in the Turczaninow herbarium, which I have not seen. The description does not come even close to fitting any Bridges specimen of *Mathewsia* I have studied from the British Museum, Kew, Geneva or Gray, all of which have substantial if not complete sets of Bridges' Chilean collections. Since neither flowers nor fruit were described by Turczaninow, the description is not very helpful in trying to locate the proper application of the name. At this time, I have not been able to determine to what species of plants (in *Mathewsia* or out) the name *M. linearifolia* applies.

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Washington. These materials and the specimens in the Gray Herbarium are cited according to the abbreviations given by Lanjouw and Stafleu (1964).

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WOOD ANATOMY OF THE GENUS EUPLASSA AND ITS RELATION TO OTHER PROTEACEAE OF THE GUIANAS AND BRAZIL

ALBERTA M. W. MENNEGA
(Botanical Museum and Herbarium, Utrecht)

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Abstract

Three genera of the *Proteaceae* belonging to the tribe *Grevilleeae* occur in the Guianas and Brazil: *Roupala*, *Panopsis*, and *Euplassa*. The microscopical wood structure of one of these genera, *Euplassa*, has not been described before. Anatomically it proves to be nearly identical with *Panopsis* which it also resembles in general properties. *Roupala* differs in several respects. Within the genera differences are not fundamental and chiefly a matter of numbers and dimensions. A key to the genera is given.

The relation of these three genera with the two other members of the tribe in South America, *Orites* and *Gevuina*, is discussed.

Introduction

With the exception of Manieri (1958) who included one unidentified species of *Adenostephanus* (a synonym of *Euplassa*) in his key to the principal timbers of Brazil, none of the handbooks or publications dealing with the anatomy of South or Central American woods mention the wood of *Euplassa* (Acosta-Solis, 1960; Bascopé, 1962; Kribs, 1928; Record and Mell, 1924; Record and Hess, 1943; Williams, 1936)[1]. Miss Chattaway (1948a) in her detailed study of the wood anatomy of the *Proteaceae* did not treat *Euplassa*, this genus not being considered to comprise any species developing into sizable trees. Neither did Metcalfe and Chalk (1950) give any particulars about the genus in their account of the family. As our material contains several samples of *Euplassa* from large forest trees as well as samples from small trees, it seemed interesting to study the wood of this genus and to compare its structure with that of other genera of the *Grevilleeae*.

Furthermore it may be worth-while to note whether the results of comparison of the wood anatomy are in agreement with the views of Johnson and Briggs (1963) on the taxonomic interrelationship of the genera.

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[1] Benoist (1931) cited *Euplassa* among the genera of the *Proteaceae* known from French Guiana, but he did not give a description of the wood of this genus nor of the other genera.

MATERIAL AND METHODS

All wood specimens studied have been collected with herbarium vouchers. Most of the herbarium specimens, either originals or duplicates, are in the herbarium of the Utrecht Institute [U]. Nearly all specimens from Brazil belong to collections identified by SLEUMER (1954) and are cited in his treatment of the American *Proteaceae*; other specimens, mainly from Suriname and French Guiana, were identified by myself. The wood samples are cited fully with particulars about tree sizes at the end of the descriptions of each genus.

As far as possible the wood sections were prepared by microtome without previous treatment except boiling. Treatment with hydrofluoric acid was necessary only for *Roupala*. Stained and unstained sections as well as macerations were prepared. In order to make the presence of silica inclusions more noticeable sections were treated with crystalline phenol followed by eugenol.

For the testing of burning qualities a match-size splinter was taken from the heartwood.

The terminology of the descriptions agrees partly with the Glossary of the International Association of Wood Anatomists (1957), and is partly adapted to the special needs of this family. For classification of numbers and dimensions the recommandations of the Council of the International Association of Wood Anatomists (1937, 1939) have been followed. Besides average data for numbers and sizes the generally occurring lowest and highest figures have been added in brackets. Instead of the usual counting of the rays per mm on a tangential surface the uniseriates have been counted per sq. mm on a tangential section.

For the drawings of elements of macerated material a camera lucida with a magnification of 148 × was used. The photographs of the transverse surfaces at 10 × magnification were made from the blocks used for sectioning.

ANATOMY OF THE FAMILY

The main features of Proteaceous woods which can be observed by hand lens are:
Rays very wide and several millimeters high, conspicuous on all surfaces; vessels partly in tangential multiples or in tangential chains, always in contact with parenchyma bands which are contiguous with the vessels on their abaxial sides; the bands narrow, numerous, and parallel, usually more or less convex, with the concave side facing the bark, running as festoons between the broad rays; the vessels hardly ever in contact with the broad rays²).

However, in two of the three genera treated here (*Euplassa* and *Panopsis*) the characteristic pattern is less pronounced, because the

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²) For microscopical details, see the paragraph: Remarks on the anatomy.

vessels are scarce and scattered, and the parenchyma bands, moreover, are often independent of the pores and nearly straight.

No generic descriptions are included. Though the differences between the species of one genus are not very important (as may be concluded from the descriptions of the species), the discrepancy between the number of species studied and the actually known numbers as given by SLEUMER (1954) does not seem to permit a detailed generic account. *Roupala* has 51 species, *Panopsis* 11, and *Euplassa* 20 species; of these 4, 2 and 4 respectively, were studied. The most important structural differences between the genera may be taken from the key.

KEY

1.a. Every parenchyma band associated with solitary vessels or vessel groups; fibres very thick-walled with extremely narrow lumen; intervascular pits 2–4 μ; average length of vessel members 500 μ . . . . *Roupala*

b. Parenchyma bands partly not associated with vessels; fibres moderately thick-walled with a lumen equal to or mostly exceeding the thickness of the walls; intervascular pits medium-sized; vessel members on the average 900 μ long 2

2.a. Uniseriate rays often over 6 cells high; parenchyma strands often consisting of 6 or 8 or more cells . . . . *Panopsis*

b. Uniseriates rarely over 4 cells high; parenchyma strands mostly of 4 cells . . . . *Euplassa*

EUPLASSA Salisb.

Euplassa pinnata (Lam.) Johnst. (Plate I, fig. 1; Plate II, fig. 3; Plate III, A)

(syn. *Adenostephanus guianensis* Meisn.)

Heartwood pinkish brown, clearly differentiated from the cream-coloured, 1.5 to 3.5 cm wide sapwood; the wide rays very conspicuous on all surfaces, producing a silvery ribbon pattern on radial surfaces; texture rather coarse; grain straight; volume weight 0.60–0.70; a splinter of the heartwood burns in 4 out of 5 samples to grey ash, in Uw 4722 to charcoal.

Wood structure

Growth rings: Absent.

Vessels: A variable percentage solitary, others in tangential pairs or tangential rows of 3–4 (7) or in small clusters, rarely in radial pairs, scattered though often with a tendency to tangential arrangement, on average 5 (0–10) per sq. mm, in Uw 4722 more variable and in some places crowded, 9–18 per sq. mm; cross-section roundish or oval with greatest dimension tangentially, at least for solitary vessels;

tangential diameter on average 150 (75–250) μ but rather variable for the various samples, in the clusters often narrower; vessel elements on average 880 (690–1070) μ long, "tails" included, often of irregular form; perforations usually large, nearly horizontal or slightly oblique, sometimes in the narrow vessels as small openings in the lateral walls; wall 5–7 μ thick; intervascular pits alternate, nearly round, 6–7 μ, apertures included; occasionally with yellowish resinous contents.

Tracheids: Often present, associated with the vessel clusters, diameter 30–60 μ, length 800–1000 μ.

Fibre tissue: Walls moderately thick (5–8.5, μ), lumen always wider than the thickness of the walls, generally much wider, diameter 20–45 μ, fibre length on average 2430 (1500–3850) μ, in Uw 5754 the average length 3350 μ; pits with very small borders and extended slitlike apertures, ca. 7 μ long, equally numerous on radial and tangential walls.

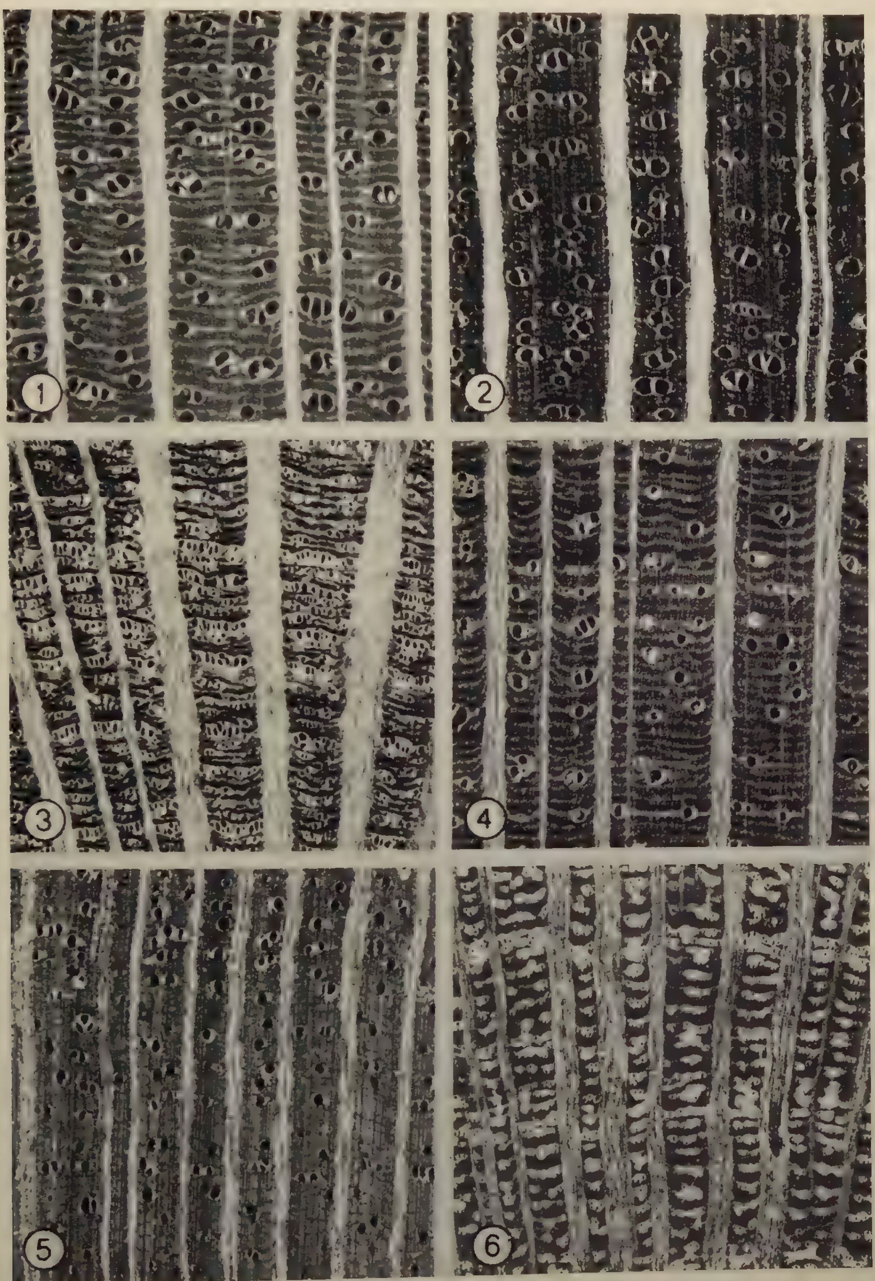
Rays: Of two sizes: uniseriates, composed of 1 to 2, or up to 4 square or upright cells, the upright cells mostly 100–160 μ axially; multiseriates mostly 10–15 (6–22) cells wide (or 325–450 μ and up to 800 μ); mostly 7–8 cm high, in Uw 5754 up to 1.5 cm; composed of procumbent cells of variable sizes, radially elongated low cells irregularly mingled with much shorter and higher, almost square cells, on tangential sections widest cells often more numerous in the middle of a ray; sheath cells locally present; margins usually formed by one, occasionally 1–4 rows of square or upright cells, the latter not over 150 μ high; pits to vessels rather scarce as the rays are rarely in contact with vessels, similar to the intervascular pits or larger and elongate; cells often with reddish brown contents, which may be concentrated around silica bodies; in one sample (Uw 1905) several rays with sclerified cells (Plate II, 3). Uniseriates 2–5 per sq. mm, wide rays 8–10 per cm.

Parenchyma: Predominantly banded, the bands partly associated with the vessels and vessel multiples in a very characteristic way adjoining them laterally and on the abaxial sides; the bands mostly 1–2 (4) cells wide, running, one pore width apart, fairly straight or slightly curved between the large rays, a few bands interrupted or ending blindly; paratracheal parenchyma may be present, beside where the bands are contiguous with the vessels as a few cells on the adaxial sides of the vessels or as a vasicentric ring of one cell layer; number of bands variable, on average 7 (5–10) per mm; strands mostly of 4 (2–8) cells; pits to vessels half bordered, generally similar to the intervascular pits, in part much larger and elongate; cells often with brown contents, sometimes with small silica bodies.

OTHER SPECIES

Wood specimens of three other species were available: *Euplassa madeirae* Sleum., *E. cantareirae* Sleum., and *E. inaequalis* (Pohl) Engl.

The samples of these species are nearly identical with *E. pinnata*



Transverse surfaces 10 ×.

Fig. 1. *Euplassa pinnata* (Lam.) Johnst. (Uw 5697); fig. 2. *Euplassa inaequalis* (Pohl) Engl. (Uw 7647); fig. 3. *Euplassa cantareirae* Sleum. (Uw 6920); fig. 4. *Panopsis sessilifolia* (Rich.) Sandw. (Uw 5810); fig. 5. *Panopsis rubescens* (Pohl) Pitt. var. *simulans*. Macbride (Uw 8264); fig. 6. *Roupala rhombifolia* Mart. (Uw 6919).

Plate I

Facing p. 120.

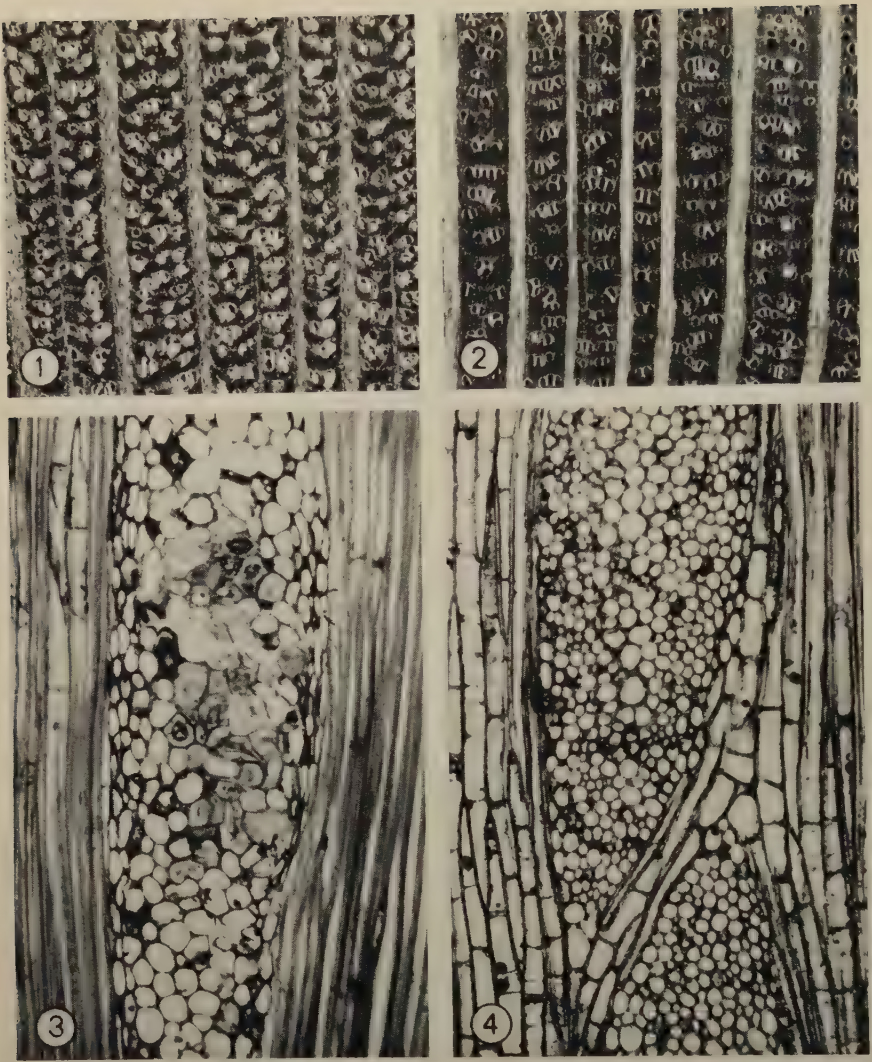
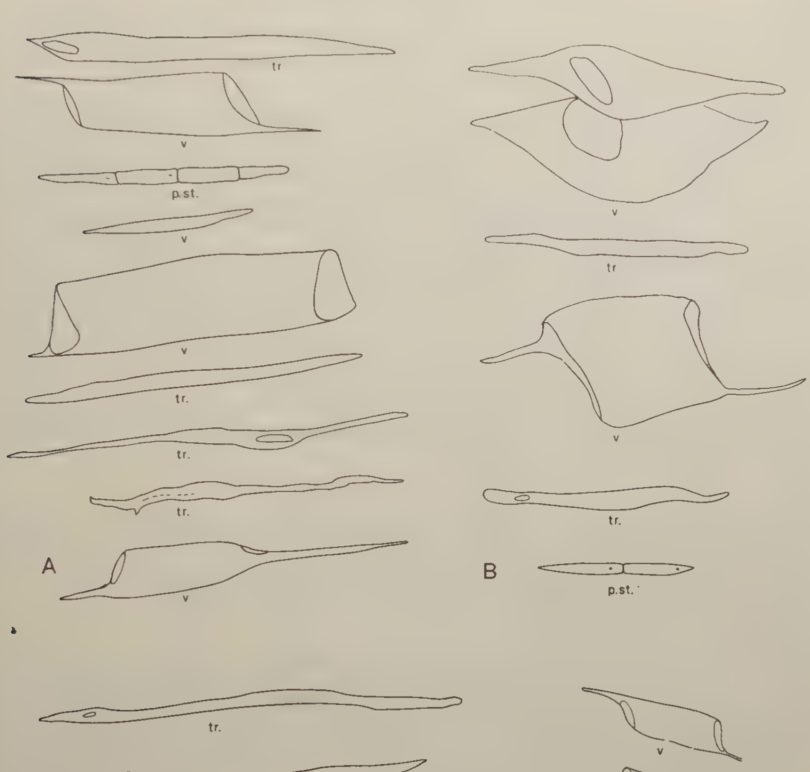


Fig. 1. *Roupala montana* Aubl. (Uw 249) transv. surf. 10 × ; fig. 2. *Roupala dielsii* Macbride (Uw 7833) transv. surf. 10 × ; fig. 3. *Euplassa pinnata* (Lam.) Johnst. (Uw 1905) tang. sect. 77 ×, large ray with sclerotic cells; fig. 4. *Panopsis sessilifolia* (Rich.) Sandw. (Uw 5810), tang. sect. 77 ×, superposed large rays separated by a few parenchyma strands.

Plate II.



Elements from macerated material, 148 ×.
p. st. parenchyma strands, tr. tracheids, v. vessel elements
A *Euplassa pinnata* (Lam.) Johnst.; B. *Euplassa madeirae* Sleum.; C. *Panopsis sessilifolia* (Rich.) Sandw.; D. *Roupala montana* Aubl.

Plate III

in general properties. Their volume weights are between 0.60 and 0.65; a splinter of the wood of *E. madeirae* burns to charcoal, splinters of the other samples burn to grey ash.

In anatomy there is close agreement between *E. inaequalis* (Plate I, fig. 2) and *E. pinnata*, except for the absence of silica inclusions.

E. cantareirae (Plate I, fig. 3) differs from *E. pinnata* in having more numerous and smaller vessels, on average 30 (14–55) per sq. mm, and 60 (20–100) μ wide, moreover arranged in long tangential chains between the broad rays. Furthermore the diameter of the fibres is on average 17 μ, max. 25 μ instead of the average of 30–35 μ in all other species; the large rays may be up to 26 cells wide; owing to the more numerous tangential chains of vessels the parenchyma bands are nearly always associated with the vessels.

E. madeirae (Plate III, B) has equally wide rays as *E. cantareirae*, in which silica bodies are apparently absent, otherwise the structure is similar to *E. pinnata*.

MATERIAL

Euplassa cantareirae Sleum.: *Brazil* – Uw 6920 (Reitz & Klein 6370 = HBR. 16373, Santa Catarina; 10 m high, diam. 5 cm).

Euplassa inaequalis (Pohl) Engl.: *Brazil* – Uw 7647 (Krukoff 6329 = USw 7647, Amazonas; tree 48 m high).

Euplassa madeirae Sleum.: *Brazil* – Uw 8167 (Krukoff 7086 = USw 8167, *type* Amazonas; tree 25 m high).

Euplassa pinnata (Lam.) Johnst.: *Suriname* – Uw 1905 (Lanjouw et Lindeman 2759, Nassau Mts; tree 9 m high, diam. 5 cm); Uw 4722 (Lindeman 7007, Nassau Mts; tree 18 m high, diam. 36 cm); *French Guiana* – Uw 5697 (BAFOG 1208, Cayenne; tree 32 cm diam., "lamoussaie blanc"), Uw 5754 (BAFOG 1266, Cayenne; tree 32 cm diam., "bois grage blanc"); *Brazil* – Uw 8969 (Terr. Federal de Amapá, Araguari 51685; diam. approx. 12 cm).

PANOPSIS Salisb.

Panopsis sessilifolia (Rich.) Sandw. (Plate I, fig. 4; Plate II, fig. 4; Plate III, C).

Sapwood greyish white to cream-coloured, 1.5–3 cm wide, clearly differentiated from the pinkish brown heartwood, lustre moderate, radial surfaces with an attractive ribbon pattern due to the conspicuous high rays; texture moderately coarse, grain straight; volume weight 0.63–0.69; a heartwood splinter burns to dark grey ash or to charcoal.

Wood structure

Growth rings: Absent.

Vessels: For 50 % or more solitary, the others in tangential pairs or in small clusters consisting of a few wide and several narrow vessels or tracheids, radial pairs rare; scattered, sometimes locally more numerous, on average 2–4 (0–12) per sq. mm; cross section round or oval with largest diameter in tangential direction, slightly angular, diameter variable, mostly 100–150 (45–230) μ; vessel members often strongly caudate or of irregular form, on average 900 (500–1350) μ long, longest in the sample with the widest vessels, perforations usually large and horizontal but also strongly oblique or occuring in lateral walls, in the narrow vessels often very small, oblique and one-sided; wall thickness 3–6 μ; pits alternate, oval, 7 μ wide, apertures included; sometimes with brown contents.

Tracheids: Present in several samples, diameter on average 45 (25–60) μ, length equal to vessel members.

Fibres tissue: Fibres with thin to moderately thick walls, 4–7 μ, lumen at least as wide and mostly much wider than wall thickness, diameter 30 (18–40) μ; length on average 2140 (1500–2880) μ; pits with small borders and slit-like extended apertures (5 μ), numerous on radial and tangential walls.

Rays: Of two sizes; uniseriates composed of upright and square cells, occasionally also a few procumbent cells present, the upright cells 60 to 100 μ axially, number of cells mostly 1–8 (15); multiseriates 6–20 cells wide, mostly 200–300 (600) μ wide, height generally 4–5 mm, up to 7 mm; composed of procumbent cells of strongly variable dimensions, mostly radially elongated (120–240 μ) and very low (17 μ), but mixed with much higher and shorter, nearly square cells, on tangential section of very irregular sizes (Plate II, fig. 4); sheath cells locally; margins sometimes composed of one row of square cells, rarely of 2–3 rows, often two or even more rays nearly vertically superposed separated by only one or two oblique fibres or parenchyma strands (Plate II, fig. 4); cell walls usually heavily pitted, pits to vessels extremely scarce; cells often with reddish brown contents, in all samples small silica bodies are present; number of uniseriates 4 per sq. mm, in Uw 4399 11 per sq. mm, wide rays 5–10 per cm.

Parenchyma: Predominantly banded, the bands partly associated with the vessels – running in 1–2 (3) cells wide fairly straight, though slightly convex bands between the wide rays, occasionally bands interrupted; when in contact with vessels or vessel groups contiguous on the lateral and abaxial sides, or exclusively on the abaxial sides, a few paratracheal cells often present on the adaxial sides or the vessels completely enclosed by a vasicentric ring of one layer of cells; number of bands 6–8 per mm; strands mostly of 4–8 (2–12) cells; pits to vessels similar to the intervascular pits or larger and elongate; cells often with brown contents and small silica bodies.

OTHER SPECIES

Panopsis rubescens (Pohl) Pittier var. *simulans* Macbride (Plate I, fig. 5). The wood of this species closely resembles *P. sessilifolia* in its general characters, except for the greater volume weight (0.81). In anatomical structure it is very similar, except for the fibres which have slightly thicker walls and a narrower lumen, diameter on average 25 μ, and for the absence of silica bodies in the cells of the rays or the parenchyma.

MATERIAL

Panopsis sessilifolia (Rich.) Sandw.: *Suriname* – Uw 291 (Stahel, Wood herbarium 291, Saramacca R.; diam. unknown, over 13 cm), Uw 4399 (Lindeman 6413, Coppename R. near Bitagron; high 14 m, diam. 9 cm). *Brit. Guiana* – Uw 1039 (For. Dept. 3040, diam. unknown, over 16 cm); sections Yale 9476 (Persaud 71). *Fr. Guiana* – Uw 5810 (BAFOG 1322, Cayenne; diam. ca. 65 cm).

Panopsis rubescens var. *simulans* Macbride: *Suriname* – Uw 1960 (Lanjouw & Lindeman 2872, Nassau Mts; tree 25 m high, diam. 30 cm). *Brazil* – Uw 8264 (Krukoff 7236 = USw 8264 Amazonas, Humayta, tree 15 m high, ca. 19 cm diam.).

ROUPALA Aubl.

Roupala montana Aubl. (Plate II, fig. 1; Plate III, D)

Sapwood greyish brown with reddish hue, not clearly differentiated from the purplish brown heartwood, rather dull but with an attractive pattern on radial surfaces due to the prominent high rays with their silvery gloss; texture rather fine, grain straight; volume weight 0.83; a splinter of the heartwood burns to ash.

Wood structure

Growth rings: Absent.

Vessels: Predominantly solitary but also in radial pairs or more often in tangential pairs or multiples, occasionally in small clusters; in tangential arrangment accentuated by the association of all vessels on their abaxial sides with parenchyma bands; on average 19 (11–31) per sq. mm; cross section roundish or oval with longest axis in radial direction; tangential diameter on average 100 (40–140) μ; vessel members rather often with long tapering "tails", medium-sized, 500 (260–600) μ long; perforations usually large and nearly horizontal, sometimes in a lateral position; cell wall 5 μ thick; intervascular pits crowded, alternate, very fine (4 μ), generally with coalescent apertures giving the impression of helical sculpturing of the vessel wall; occasionally with yellow contents.

Tracheids: Extremely scarce; of about the same length as the vessel members and mostly 35 μ wide.

Fibre tissue: Fibres with thick walls (8–13) μ, lumen hardly visible, diameter 17–27 μ; moderately long, on average 1830 (1500–2190) μ; pits with very small borders and rather short slit-like apertures, more numerous on radial than on tangential walls.

Rays: Nearly exclusively multiseriate; uniseriates scarce, composed of 1–2 (4) rows of square or upright cells, the latter mostly 70–100 μ long axially; multiseriates 7–25 cells wide (100–460 μ); mostly 4–5 mm high and up to 6 mm; consisting entirely of procumbent cells of various dimensions, usually with one, occasionally 2–4 marginal rows of square cells; sheath cells sometimes present; cells rather thick-walled; pits to vessels scarce, similar to the intervascular pits; cells often with reddish brown contents, small silica bodies often present. Number of uniseriates 2–4 per sq. mm; broad rays 9 per cm.

Parenchyma: In concentric convex bands, 1–4 cells wide forming a festoon between the broad rays, all bands in contact with vessels and vessel multiples lining them exclusively on their abaxial sides; rarely a few cells paratracheal parenchyma on the adaxial sides; number of bands 3–4 per mm; strands mostly of 4–6 (2–8) cells; pits to vessels similar to the intervascular pits; cells usually with reddish brown contents, and often with small silica bodies.

OTHER SPECIES

Material was available of *R. cataractarum* Sleum., *R. dielsii* Macbride, and *R. rhombifolia* Mart.

In their *general properties* the agreement of all specimens with *R. montana* is very close. The *wood structure* resembles also rather closely this species, the chief differences being found in numbers and dimensions of the vessels, occurrence of tracheids, width of the parenchyma bands, and in the presence or absence of crystals, stone cells, and vertical resin ducts.

In *R. cataractarum* the vessels are more numerous, on average 30 (20–40) per sq. mm; diameter on average 47 (20–80) μ; very small silica bodies often present in the procumbent ray cells; parenchyma bands mostly 4 cells wide and sometimes enclosing the vessels completely or at least a few cells of paratracheal parenchyma present on the adaxial faces of the pores.

In *R. dielsii* (Plate II, fig. 2) the two samples are nearly identical with *R. montana* and mutually much alike except for the stone cells in the wide rays present in Uw 7545, and apparently absent in the other sample. Differences with *R. montana* are the occurrence of small rectangular crystals in some of the procumbent ray cells, and occasional axial ducts of the same diameter as the vessel diameter which could be traced in both samples.

In *Roupala rhombifolia* (Plate I, fig. 6) the vessels are numerous, on average 50 per sq. mm, narrow, and mostly arranged in long tangential multiples, intervascular pits 2 μ; tracheids numerous; the wide rays contain several clusters of sclerotic cells, and in some of the procumbent cells small rectangular crystals are present; the parenchyma is completely restricted to the abaxial, mostly 2 (4) cells wide bands.

MATERIAL

Roupala cataractarum Sleum.: *Brazil* – Uw 6918 (Reitz 6030 = HBR 16371, Santa Catarina; 4 m high, diam. 3.5 cm).

Roupala dielsii Macbride: *Brazil* – Uw 7545 (Krukoff 6194 = USw 7545, Amazonas; tree 15 m high); Uw 7833 (Krukoff 6633 = USw 7833, Amazonas; tree 21 m high).

Roupala montana Aubl.: *Suriname* – Uw 249 (Stahel, Wood herb. 249, Zanderij I; diam. 12 cm or more, "warirodan").

Roupala rhombifolia Mart.: *Brazil* – Uw 6919 (Reitz & Klein 6367 = HBR 16372, Santa Catarina; 10 m high, diam. 6 cm).

REMARKS ON THE ANATOMY

Tracheary elements. In all species investigated the perforations are simple, usually large and terminal, but sometimes oblique and lateral; in the narrow elements perforations are often very small. Those elements resemble closely the vascular tracheids of the same dimensions with one or without any perforation. Vascular tracheids tend to be more numerous in specimens with the smallest vessel diameter and with numerous clusters. The form of the vessel elements may vary a great deal; the often very long and tapering "tails" are another characteristic feature of the investigated species (Plate III). The length of the tracheary elements is well above medium-size in *Panopsis* and *Euplassa*, where even a maximal fibre length of 3800 μ was observed in one sample.

Ray tissue. The very wide and high rays accompanied by a few very low uniseriates, which are not over a few cells high, form another character present in the three genera. The remarkable variation in the dimensions of the procumbent cells composing the wide part of the broad rays is more conspicuous in *Panopsis* and *Euplassa* than in *Roupala*, because in the latter genus the largest cells are nearly half the size of the largest cells in the two other genera. Upright cells occur in the uniseriates, in the marginal rows and occasionally as sheath cells; usually the axial dimension of these cells is not over three times the radial dimension.

The suggestion of axially superposed rays brought about by the "intersection" of large rays by a few oblique fibres or parenchyma strands (Plate II, fig. 4) is another feature common to all samples. It is very likely that new rays are formed here by the splitting of the wide rays, a process described by Miss Chattaway (1933) for the *Sterculiaceae*. She suggested herself that a similar process might take place in the Grevilleoideae (Chattaway, 1948a); this was afterwards confirmed for the rays of *Banksia* (Chattaway, 1948b). Sclerotic ray cells were found in one specimen of *Roupala dielsii* and in *R. cataractarum*, also in one of the samples of *Euplassa pinnata*, but not in *Panopsis* for which genus Chattaway (1948a) reported the occurrence of these cells. Small silica aggregates were observed in nearly all specimens though they were more numerous in one sample than in another. Their presence is often obscured by the accumulation of brown or orange cell contents around them. The dimensions of the silica bodies are variable, but usually not over 8 μ; occasionally small particles like the crystal sand of silica described by Bamber and Lanyon (1960) in *Stenocarpus sinuatus* were observed. Small rectangular crystals were exclusively found in two species of *Roupala*. Oil cells reported to occur in *Roupala* (Williams, 1936) have not been found.

Parenchyma. It is rather difficult to say whether the banded parenchyma must be interpreted as apotracheal or paratracheal. In *Panopsis* and *Euplassa* those bands which are not connected with the vessels meet the requirements of apotracheal bands but the other bands, otherwise essentially similar except for their contact with the vessels, should be considered paratracheal. In my opinion the bands in contact with the vessels on their abaxial sides do not correspond to paratracheal parenchyma. I preferred therefore the term banded without further specification. As truly paratracheal I regard the cells or partial rings on the adaxial sides of the vessels. Chattaway (1948a) described the parenchyma lines in *Panopsis* as primarily apotracheal, reticulate, and as paratracheal in *Roupala*, where all the bands are associated with the vessels. She based her key to the genera of the *Grevilleoideae* on this devision. She stated, however, in her discussion of the parenchyma distribution that the fundamental difference between the two types may be obscured when the bands are numerous and fine, and when at the same time the vessel chains are equally numerous so that practically no parenchyma bands are independent of the vessels. An example of such a type of parenchyma distribution is found in *Euplassa cantareirae* (Plate I, fig. 3), which has more numerous vessel chains than the other species of *Euplassa*.

Axial ducts. Intercellular canals of probably traumatic origin were observed in both samples of *Roupala dielsii*. The occurrence of these structures was reported for several Australian genera but so far not for any American species.

Discussion

The descriptions of the wood anatomy and the key show that the structure of *Euplassa* is nearly identical to that of *Panopsis* while *Roupala* differs in various fundamental characters. It even seems quite well possible that further study of more species of both *Euplassa* and *Panopsis* would show the slight variation in the numbers of cells of the uniseriate rays and in the parenchyma strands, as well as the differences in the height of the broad rays, not to be a constant and reliable character for distinguishing the two genera.

Other genera belonging to the tribe *Grevilleeae* in South America are *Orites* (2 species) and *Gevuina* (1 species), both restricted to the Andean chain. No wood sample was available of *Orites*. Another member of the genus, *Orites excelsa* R. Br., occurring in Australia, was studied by Miss Chattaway (1948a). She described the wood structure as identical with that of *Knightia excelsa* R. Br., a member of the *Embothrieae*. This implies that in general the structure resembles *Panopsis* except for the parenchyma bands which are always in contact with the vessels, and for the vessels arranged mostly in tangential chains.

Of *Gevuina avellana* Mol. a wood sample and detailed descriptions (Tortorelli, 1956; Wagemann, 1948) were available. The structure has more affinity to *Panopsis* and *Euplassa* as far as the histology of the elements is concerned, e.g. the medium-sized intervascular pits, the relatively thin walled fibres with a large lumen. However, the arrangement of the vessels in long tangential chains and the constant association of all parenchyma bands with the vessel chains is again an indication that this species does not belong to the same group as *Panopsis* and *Euplassa*.

Considering exclusively the American members of the *Grevilleeae* the conclusion should be that in terms of wood structure *Panopsis* and *Euplassa* are very closely related; *Gevuina* and probably *Orites*, may be regarded as intermediates between them and *Roupala*.

This result is not in agreement with the suggested evolutionary relationships based on comparative morphology published by Johnson and Briggs (1963) who believe *Roupala* to be most closely related to *Panopsis*, and *Euplassa* to *Gevuina*. These authors placed *Orites* in a different tribe.

However, in the *Proteaceae* wood structure is probably less important for deciding the limits of taxa above the rank of genus than for determining the position of a species within a genus, e.g. the discrepancies found by Janssonius (1930) within the genus *Helicia*, and Sleumer's (1955) description of a new genus, *Heliciopsis*, in which inter alia the two aberrant species were placed.

Chattaway (1948a) noted two other aberrant species among her material of *Helicia*, one of them *H. diversifolia* White, with the same type of wood structure as the species now referred to *Heliciopsis*. However, *Helicia diversifolia* White, which species according to Sleumer (1955) did not fit in *Helicia* was transferred by him to the monotypic genus *Hicksbeachia*. Here it seems rather out of place from the point of view of wood anatomy since *Hicksbeachia pinnatifolia* F. Muell., the other species, differs according to Miss Chattaway's description in several respects from the structure of *Helicia diversifolia*. However, Dr. Sleumer (personal communication) no longer holds the view that *Helicia diversifolia* is congeneric with *Hicksbeachia*. No taxonomic information was available to me on the other species cited by Miss Chattaway, *Helicia montana* Sym.

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NOTES ON THE ARACEAE OF SURINAM III[1]

A. M. E. JONKER–VERHOEF AND F. P. JONKER
(Botanical Museum and Herbarium, Utrecht)

(received November 15th, 1965)

After the publication of part I and part II of this series a number of Aroids were collected in the interior of Surinam, chiefly by A. G. H. Daniels and F. P. Jonker during an expedition to the Emma Range in 1959. The following is an enumeration of species collected for the first time in Surinam in addition to records of recollections of rare taxa and critical notes on misinterpreted or confused species. The present authors also examined those specimens collected by J. van Donselaar and W. A. E. van Donselaar-ten Bokkel Huinink (1958/59), K. U. Kramer and W. H. E. Hekking (1960/61), J. G. Wessels Boer (1963), J. P. Schulz (1963) and P.A. Florschütz and P. J. M. Maas (1964/65).

Dracontium L.

Dracontium foecundum Hook. f. was collected for the first time in Surinam by P. A. Florschütz and P. J. M. Maas. The species was hitherto known from British Guiana and Trinidad only.

It is closely related to *D. asperum* K. Koch, differing only in its much longer peduncle (30 cm or more) which in *D. asperum* is about as long as the spathe (up to 15 cm).

For description and literature, see Jonker and Jonker in Flora of Suriname 1 pt. 2, 1953, p. 7–8.

Lower Suriname Riv., plant. Peperpot (Florschütz and Maas 3162, fl. March 1965 [U]).

Cyrtosperma Griff.

Up till now a single species – *C. spruceanum* (Schott) Engl. – was known from Surinam and only collected on a single occasion. Another species was only known from French Guiana and has now been found in S. Surinam as well.

Cyrtosperma americanum Engl. in Mart., Flor. Bras. III. 2 (1878), p. 117, tab. 22; Engler in D.C., Mon. Phan. II (1879), p. 272; Engler, Das Pflanzenreich IV. 23 C (1911), p. 22, Fig. 8.

Terrestrial herb; each plant provided with a single leaf and an inflorescence. Leaf blade sagittate-tripartite, herbaceous, up to 60 cm wide. Apical lobe triangular, up to 38 cm long, pinnatipartite; lateral

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[1] Part I in Acta Botanica Neerlandica 2, 1953, p. 349–362 (also published as Mededelingen van het Botanisch Museum en Herbarium, Utrecht, no. 118); part II in Acta Botanica Neerlandica 8, 1959, p. 139–155 (Mededelingen no. 154).

segments up to 20 cm long and 6 cm wide, often forked at the apex; apical segment elongate-rhomboid, up to 20 cm long and 17 cm wide. Basal lobes on the exterior side of their main ribs pinnatifid, on the inner side entire, up to 30 cm long. Sinus between the basal lobes penetrating to the main ribs of the latter, the denudate part up to 5 cm long. Petiole rough, brown-blotched, up to 130 cm long; basal part vaginate, 10–20 cm long. Peduncle rough, especially in the basal part, up to 110 cm long. Spathe white, tinged with purple in the basal part, or brown-purple, up to 25 cm long; the apical part spirally twisted, acute, shortly subulate. Spadix stipitate, shortly cylindrical, obtuse, up to 3.5 cm long and 0.7 cm in diameter; stipe 1–2 cm long. Tepals 4, cucullate, circ. 2.3 mm long and 2–2.3 mm wide. Filaments rather broad, ribbon-shaped, circ. 2 mm long and 1–1.8 mm wide; anthers circ. 0.6 mm long. Ovary ovoid to pear-shaped, circ. 2.3 mm long and 1.8 mm wide, 1-locular with a single, basal ovule.

Distribution: French Guiana.

Junction of Paloemeu Riv. and Tapanahoni Riv., in marshy creek valley among shrubs (Wessels Boer 1223, fl. Apr. [U]).

This species differs from *A. spruceanum* in the basal lobes of the tripartite leaf. These are pinnatifid on both sides of their main ribs in *C. spruceanum* and entire on the inner side and pinnatifid on the exterior side of their main ribs in *C. americanum*. The ovary contains 2 ovules in *C. spruceanum* and 1 in *C. americanum*. The seeds are smooth in *C. spruceanum* and cristate in *C. americanum*.

Anthurium Schott

1. *Anthurium crassinervium* (Jacq.) Schott, a species already collected three times in the interior, appeared to be rather common in the Emma Range on bare rock, both dolerite and granite. *Vid.* I, p. 352. II, p. 139.

Daniëls and Jonker 807, 1285, 1286 [U].

2. *Anthurium huegelii* Schott. As mentioned before (I, p. 322) *Anthurium crassinervium*(Jacq.) Schott was often confused with *A. hookeri* Kunth and in the latter Engler wrongly included *A. huegelii* Schott. We agree with N. E. Brown (1910) and Simmonds (1950) in considering this a distinct species. It was collected in Surinam for the first time in the Emma Range and later on in the Wilhelmina Mountains also.

Anthurium huegelii Schott, Prodr. (1860), p. 469; N. E. Brown in Gard. Chron. 48 (1910), p. 153; Simmonds in Kew Bull. (1950), p. 395; Jonker and Jonker in Act. Bot. Neerl. 2 (1953), p. 352; — *Anthurium trinitatis* Engl., Das Pflanzenr. IV. 23 B (1905), p. 73.

A usually epiphytic rosulate herb, according to Schulz also terrestrial (In Trinidad, according to Simmonds saxicolous in the drier districts and epiphytic on trees in the moister ones). Petiole sulcate, 5–19 cm long; joint 0.6–1.5 cm long. Leaf blade subcoriaceous, spathulate, acute and mucronate at the apex, decurrent to obtuse at base, 75–90 cm long and 21–31 cm wide. Peduncle slender, 40–75 cm long. Spathe lanceolate, mucronate, amplectant, 5–19 cm long and 0.8–2 cm wide, green tinged with red outside. Spadix almost sessile, narrowly cylindrical, 8–27 cm long and up to 1 cm in diameter, vivid bluish-purple. Tepals cucullate, circ. 1.5 mm long and 1–1.5 mm wide. Stamens circ. 1 mm long and 0.2–0.4 mm wide. Ovary cylindrical, 2-locular, circ. 1.5 mm long and 1.5 mm in diameter; each cell containing a single ovule inserted in the middle of the dissepiment. Stigma sessile, discoid. Berries obovoid, white at base and purple at apex.

Distribution: West-Indian Islands, British Guiana.

Emma Range, Hendriktop, S slope, upper limit of cloud forest, alt. 950 m (Daniëls and Jonker 955, fl. Aug. 1959 [U]); Wilhelmina Mountains, Julianatop, alt. 1000 m (Schulz 10281, fl. Aug. 1963 [BBS, U]).

This species differs from *A. crassinervium* (Jacq.) Schott in its much shorter petiole and the subcoriaceous spathulate leaf blade which is slightly truncate at the base and, moreover, in its white with purple, obovoid berries which are scarlet and ellipsoid in *A. crassinervium*.

3. *Anthurium jenmanii* Engl., a species new to Surinam, belonging in the same group as the preceding species, characterized chiefly by its leaf shape.

Anthurium jenmanii Engl., Das Pflanzenreich IV. 23 B (1905), p. 72. Terrestrial, rosulate herb. Petiole stout, sulcate, 11–12 cm long and 1 cm in diameter; joint 0.5–1 cm long. Leaf blade coriaceous, elliptical, acute or acuminate and mucronate at the apex, rounded to truncate at the base, 48–75 cm long, 20–37 cm wide; truncate base 6–7 cm wide; midrib prominent. Peduncle 40–80 cm long and 1 cm in diameter. Spathe lanceolate, acuminate, 8–16 cm long and up to 1.5 cm wide. Spadix shortly oblique-stipitate, long and narrowly cylindrical, tapering towards the apex, purple-brown, 9–24 cm long and up to 1 cm in diameter, stipe up to 1 cm long. Sepals cucullate, circ. 1.5 mm long and 2 mm wide; petals circ. 2 mm long and 2 mm wide. Stamens circ. 2.25 mm long and 1 mm wide. Ovary cylindrical, 2-locular, circ. 2 mm long and 1 mm in diameter; each cell containing a single ovule inserted in the middle of the dissepiment. Stigma sessile, discoid.

Distribution: British Guiana, Trinidad, Colombia.

Emma Range, Wosuna fall, alt. 300 m, on granite slope (Daniëls and Jonker 833, fl. Aug. 1959 [U]).

Note: Simmonds 82 (Herb. Trinidad 13883), Trinidad, cited by Simmonds in Kew Bull. 1950, p. 395, under *A. huegelii* Schott belongs to this species and is, consequently, the first record from Trinidad. Lambert (in Claes) 2899, fl. Nov. 1926 [BR], represents the first collection from Colombia.

4. **Anthurium lanjouwii** Jonk. et Jonk., n. sp. (Fig. 1)

Herba terrestris rosulata. Caudex brevis, cylindricus ad 15 cm longus; cataphylla lanceolata ad 3.5 cm longa et 1.8 cm lata, mox in fibras tenues resoluta. Internodia ad 0.5 cm longa, 1 cm crassa. Petiolus semiteres, 7–23 cm longus geniculo ad 1 cm longo instructus. Lamina coriacea, elliptica, basi obtusa vel cuneata, apice acuminata et mucronata, 23–36 cm longa, 9–19 cm lata. Pedunculus 17–35 cm longus. Spatha lanceolata, mucronata, ad 4.5 cm longa, 0.8 cm lata. Spadix breviter stipitatus, 5–14 cm longus, 0.2–0.6 cm crassus. Ovarium 2-loculare; loculis uniovulatis.

Holotypus: Daniels et Jonker 1241 in herbario U, e Surinamo in montibus Emmaketen australibus.

Paratypi: Daniëls et Jonker 1101 in cacuminae montis IJzermantop, Emmaketen [U]; Daniëls et Jonker 1264 in montibus Emmaketen australibus [U].

Derivatio nominis: Prof. Dr. J. Lanjouw herbarii Rheno-Traiectini.

Terrestrial rosulate herb. Stem cylindrical, up to 15 cm long, densely covered by adventitious roots and lanceolate cataphylls, up to 3.5 cm long and 1.8 cm wide, or their fibrous remains. Internodes up to 0.5 cm long and circ. 1 cm in diameter. Petiole semiterete, 7–23 cm long; joint up to 1 cm long. Leaf blade coriaceous, elliptical, obtuse or, sometimes, cuneate at the base, acuminate and mucronate at the apex, 23–36 cm long and 9–19 cm wide; midrib prominent, on both sides of it 6–7 prominent lateral veins. Peduncle slender, 17–35 cm long. Spathe lanceolate, prominently mucronate, green tinged with purple, 2.5–4.5 cm long and up to 0.8 cm wide. Spadix shortly stipitate, narrowly cylindrical, purplish-brown, 5–14 cm long and 0.2–0.6 cm in diameter. Tepals cucullate, 1.1–1.3 mm long; the outer ones circ. 0.8 mm wide; the inner ones circ. 0.5 mm wide. Ovary cylindrical, 2-locular, circ. 1 mm long and 0.5 mm in diameter; each locule containing a single pendulous ovule inserted in the middle of the dissepiment. Stigma sessile, discoid. Fruits unknown.

Distribution: rather common in the Southern part of the Emma Range only, on dolerite and sand stone.

Emma Range, IJzermantop, dolerite, alt. 850 m (Daniëls and Jonker 1101, fl. Sept. 1959 [U]; id., on sheer sand-stone slope (Daniëls and Jonker 1241 (holotype) & 1264, fl. Sept. 1959 [U]).

Note: We named this new species in honour of Professor Dr. J. Lanjouw, director of the Botanical Museum and Herbarium, State University of Utrecht, who took the initiative in organizing the Scientific Expedition to the Emma Range, Surinam, 1959.

Monstera Adans.

To the 4 species, already known from Surinam, we now add a 5th, known up till now from Costa Rica only.

Monstera epipremnoides Engl. in Bot. Jahrb. 37 (1905), p. 118; Engler und Krause, Das Pflanzenreich IV. 23 B (1908), p. 113.

Internodes 1–2 cm. Petiole vaginate except in the apical, up to 2 cm long geniculate part; vaginate part 22–32 cm long. Leaf blade thickly herbaceous, ovate, acuminate at the apex, truncate to rounded at the base, slightly cuneate near the base, fenestrate when young, finally deeply pinnatifid and, sometimes, fenestrate along the midrib,

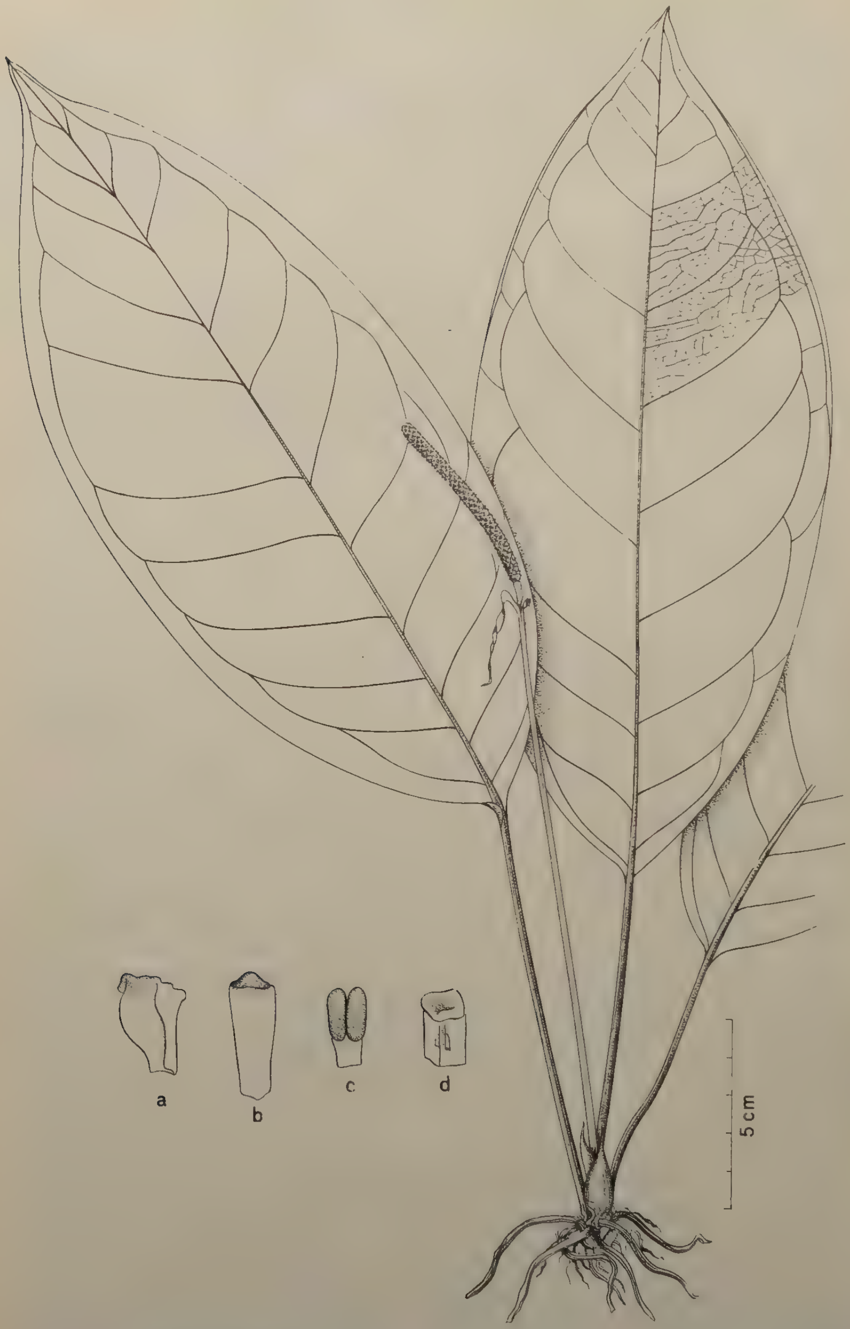

Fig. 1. *Anthurium lanjouwii* Jonk. et Jonk. a. outer tepal; b. inner tepal; c. stamen; d. pistil.

31–46 cm long and 18–27 cm wide. Pinnae falcate, except the basal ones broadened at the apex, 2–5 cm wide, provided with 1–2 principal veins, the basal pinnae with 3–4; apical lobe rhomboid. Peduncle up to 14 (—25) cm long. Spatha convolute, acuminate, deciduous, green when closed, circ. 8 cm long and 3 cm wide in the specimens from Surinam, according to Engler, l.c., 15–18 cm long and 6–7 cm wide. Spadix obliquely sessile, circ. 6 cm long in the Surinam material, according to Engler, l.c., 10 cm long. Fruit orange.

Distribution: Costa Rica.

Sipaliwini Riv., Palaime creek, in savannah forest (Wessels Boer 872, fl. and fr. March. 1963 [U]).

Dieffenbachia Schott

To the 3 species, already known from Surinam, we now add a new species.

Dieffenbachia elegans Jonk. et Jonk., n. sp. (Fig.2).

Herba erecta lignicola. Caudiculus ad 15 cm longus internodiis ad 1 cm longis. Foliorum petiolus quam lamina 2–3 plo brevior, 7–12 cm longus; vagina truncata, 5–9 cm longa, ad 1 cm lata; lamina herbacea, elliptica vel oblanceolata interdum inaequilatera vel falcata, apice apiculata, mucronulata, basi cuneata, 14–30 cm longa, 4–9 cm lata. Inflorescentia axillaris, solitaria. Pedunculus 3.5–6 cm longus. Spatha convoluta, apiculata, 10–13 cm longa, pars inferior ad 2 cm diam. Spadix sessilis; pars feminea adnata, circ. 3 cm longa, a mascula interstitio libero subnudo 2.5 cm longo separata; pars mascula libera, obclavata, circ. 2 cm longa, 0.4 cm diam. Flores femineorum staminodiis 4; ovarium rhomboideum circ. 1 mm longum et circ. 1.5 mm diam. stigmate hypocrateriformi coronatum. Florum masculorum synandria 6–7-andra, 2–3 mm diam.

Holotypus: Wessels Boer 1573 in herbario U, e Surinamo in sylva in dir. austr. a Kappel savanna prope pedem australem montis Tafelberg.

Erect herb containing a whitish latex, growing on decaying wood. Stem up to 15 cm long and up to 1 cm thick; internodes up to 1 cm long. Petiole long-vaginate, 7–12 cm long, including the tapering and truncate sheath; sheath 5–9 cm long and up to 1 cm wide. Leaf blade herbaceous, elliptical to oblanceolate, often oblique to falcate, apiculate and mucronulate at the apex, cuneate at the base, 14–39 cm long and 4.9 cm wide. Inflorescence solitary in the leaf axil. Peduncle 3.5–6 cm long. Spathe convolute, apiculate, yellowish green, turning to orange, 10–13 cm long and up to 2 cm in diameter in the basal part, opening in the apical part only. Spadix sessile; female part adenate, circ. 3 cm long and 0.3 cm in diameter; sterile part free, almost naked, circ. 2.5 cm long and 0.3 cm in diameter; male part free, obclavate, circ. 2 cm long and 0.4 cm in diameter. Female flowers scattered along the basal part of the spadix; staminodes 4, thick-scalelike, obovate, obtuse, swollen towards the apex, about half as long as the ovary; ovary rhomboid, circ. 1 mm high and 1.5 mm in diameter, crowned by an elongate, saucer-shaped stigma. Synandria consisting of 6–7 stamens, circ. 1 mm high and 2–3 mm in diameter. Fruits globose, circ. 0.5 cm in diameter.

Forest S of Kappel savannah, S of Tafelberg, along creek (Wessels Boer 1575, fl. and fr. June 1963 [U], holotype).

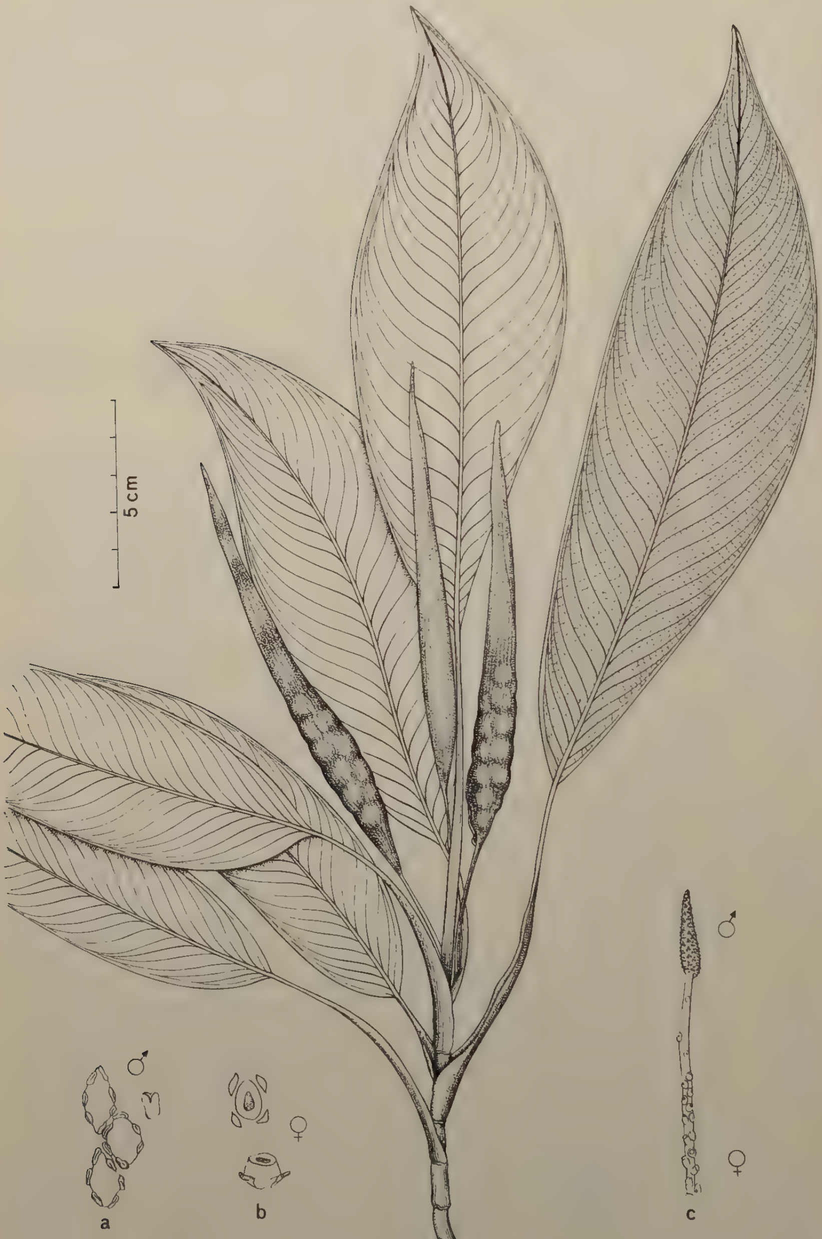

Fig. 2. *Dieffenbachia elegans* Jonk. et Jonk. a. male flowers; b. female flowers; c. spadix.

Affinities: This new species is closely allied to *D. parvifolia* Engl. from Amazonian Brazil. It differs, however, in its much longer petioles and its more herbaceous leaf blades. The leaf blades of *D. parvifolia* are coriaceous and 4–5 times as long as the petioles which are circ. 4.5 cm long. The also rather closely allied *D. humilis* Poepp. (according to Engler conspecific with *D. spruceana* Schott), known from Amazonian Brazil and Amazonian Peru differs in its leaf blades which are as long as or slightly shorter than the petioles, and by the absence of a naked sterile part of the spadix.

Xanthosoma Schott

On the basis of some recent collections we have had to change our mind with regard to the *Xanthosoma* species with sagittate-cordate leaves, generally known in Surinam as "tajer", viz.: *X. sagittifolium* (L.) Schott, *X. jacquinii* Schott and *X. belophyllum* (Willd.) Kunth.

Xanthosoma belophyllum is stemless and possesses a tuber; the sinus of the leaf blade penetrates to the main ribs of the basal lobes, producing, consequently, a denudate part of 1–2.5 cm length. The species was cited by us in Notes II (1959) under *X. jacquinii*; in Flora of Suriname (1953) we cited under *X. belophyllum* a specimen belonging, in all probability, to *X. sagittifolium*. The species is said to be cultivated as a vegetable in tropical America and this has been, probably, the case in Surinam as well as two of the three collections have been made in the coastal area. *Xanthosoma jacquinii* is characterized by a stem, 75–100 cm, crowned by a rosette of leaves. The sinus of the leaf blade penetrates to the main ribs of the basal lobes, leaving a denudate part of 2–3 cm length. The plants are provided with arm-thick, cylindrical rhizomes. As stated by SIMMONDS (1950) the species is not cultivated and occurs in damp forest.

Xanthosoma sagittifolium is characterized by a stem up to 3 m, and by its thick, elongate-tuberous to ellipsoid, angular rhizome. The sinus of the leaf blade does not penetrate to the main ribs of the basal lobes; there is, consequently, no denudate part of the basal ribs. To this species we attribute the cultivars known as "pom tajer" and "taja wirie" or "tajer blad" (tajer leaves, a leafy vegetable). Culture experiments will be needed to clarify the status of the second cultivar which is grown as a rosulate, never flowering herb.

We think it wise to give a new key to the Surinam species of this genus:

1. a. Leaves pedatifid or pedatisect 2
b. Leaves entire, either hastate or sagittate to cordate 3

2. a. Leaves pedatisect; leaflets usually 11 (5–12)
. . . . 1. *X. helleborifolium* (Jacq.) Schott
b. Leaves pedatifid, consisting of 5–9 divisions
. . . . 2. *X. hoffmannii* (Schott) Schott

3. a. Plants stemless; underground part tuberous; tubers small 4
b. Plants provided with a distinct stem; underground part rhizomatous to elongate-tuberous 5

4. a. Central part of the leaf blades rectangular; apical part triangular; basal part slightly hastate . . . . 3. *X. belophyllum* (Willd.) Kunth
   b. Leaf blades triangular, hastate, white-spotted on both sides . . . . 4. *X. conspurcatum* Schott

5. a. Main ribs of the basal lobes of the leaf blade with a 2–3 cm long denudate part in the sinus. Rhizome cylindrical. Not cultivated . . . . 5. *X. jacquinii* Schott
   b. Main ribs of the basal lobes of the leaf blade not denudate. Rhizome angular. Cultivated species . . . . 6. *X. sagittifolium* (L.) Schott

1. *Xanthosoma helleborifolium* (Jacq.) Schott – In Surinam represented by var. *variegatum* (Desf.) Engl.
   See Jonker and Jonker in Flora of Suriname I. 2 (1953), p. 50–52.
2. *Xanthosoma hoffmannii* (Schott) Schott – in Surinam represented by var. *wendlandii* (Schott) Engl.
   See Jonker and Jonker, Notes on the Araceae of Surinam II, Acta Bot. Neerl. 8 (1959), p. 141–142.
3. *Xanthosoma belophyllum* (Willd.) Kunth, Enum. III (1841), p. 114; Schott, Syn. Ar. (1856), p. 59; id., Prod. Syst. Ar. (1860), p. 184; Engler in Mart., Flor. Bras. III. 2 (1878), p. 189; Engler in DC., Mon. Phan. Prod. II (1879), p. 472; Engler u. Krause, Das Pflanzenr. IV 23. E (1920), p. 52, Fig. 9L; – non Jonker and Jonker in Flor. Sur. I. 2 (1953), p. 53; Jonk. and Jonk. in Act. Bot. Neerl. II (1953), p. 357; – *Caladium belophyllum* Willd., Enum. Plant. (1809), p. 987; — *Caladium jacquinii* auct. non Schott, Jonker and Jonker in Acta Bot. Neerl. 8 (1959), p. 143.

Plant stemless, rosulate. Leaves often bullate. Petiole up to 48 cm long, the basal 20 cm vaginate. Leaf blade herbaceous, sometimes provided with a basal, dark purple spot; central part of the leaf blade rectangular; apical part triangular, acuminate, mucronate; basal part slightly hastate; midrib of the apical lobe up to 30 cm long; main ribs of the basal lobes up to 17 cm long, their denudate part up to 2.5 cm long. Peduncle up to 19 cm long. Spathe circ. 19 cm long; limb white, circ. 12.5 cm long and 6 cm wide; tube subglobose, bluish-green, circ. 6.5 cm long and 3.5 cm in diameter. Spadix circ. 12.5 cm long, provided with an adnate, 1 cm long stipe; female part circ. 1.5 cm long and 1 cm in diameter; ovaries 3- or 4-locular, cylindrical, circ. 2 mm long, crowned by a disciform style and a cushion-shaped stigma; sterile part circ. 4.5 cm long, constricted; male part circ. 6.5 cm long, rosa-coloured.

Underground part tuberous, circ. 2.5 cm in diameter, black, inside white.

Distribution: Venezuela, Guiana, Colombia; also cultivated.

Coronie, Leasowes, along road near Sarah lake (Jonker and Jonker 550, ster. Febr. 1956 [U]); Lower Suriname Riv., plant. Peperpot (Lindeman 3694, fl.

Apr. 1953 [U]); between Coppename Riv., Right Branch, and Emma Range, in poor myrtaceous forest with lianas, alt. 300 m (Wessels Boer 1455, fl. May 1963 [U]).

4. *Xanthosoma conspurcatum* Schott
   See Jonker and Jonker in Flora of Suriname I. 2 (1953), p. 52, and the revised description in Jonker and Jonker, Notes on the Araceae of Suriname II, Acta Bot. Neerl. 8 (1959), p. 140–141, with the exception of the incorrect statement that the underground part is not tuberous. Though classified in a different section by Engler and Krause, Das Pflanzenreich IV. 23 E (1920), this species is closely related to *X. belophyllum* (Jacq.) Schott.

5. *Xanthosoma jacquinii* Schott, Melet. I (1832), p. 19; id., Syn. Aroid. (1856), p. 57; id., Prod. Syst. Aroid. (1860), p. 183; Engler in Mart., Flor. Bras. III. 2 (1878), p. 169; id., in DC., Mon. Phan. Prod. II (1879), p. 470; Hemsley, Biol. Centr. Amer. Bot. III (1885), p. 418; Engler u. Krause in Das Pflanzenreich IV. 23 E (1920), p. 47; Simmonds in Kew Bull. 1950 (1951), p. 400; – non Jonker and Jonker in Acta Bot. Neerl. 8 (1959), p. 143.

Aerial stem up to 1 m (according to SIMMONDS, l.c., up to 3 m) high, crowned by a tuft of large leaves. Petiole up to 90 cm long, vaginate in the basal part. Leaf blade herbaceous to subcoriaceous, triangular to ovate, acute at the apex, sagittate to hastate at the base; midrib of the apical lobe circ. 36 cm long; main ribs of the lobes circ. 26 cm long; their denudate part 2–3 cm long. Peduncle up to 24 cm long. Spathe circ. 14 cm long; limb white; tube purple inside. Spadix not stipitate, circ. 12 cm long; female part subglobose, circ. 1.2 cm long and 1 cm in diameter; ovaries 3-locular, cylindrical, circ. 1.5 mm long and 1.5 mm wide, crowned by a disciform style. Sterile part slender, constricted, circ. 3 cm long. Synandrodia oblong; the basal ones no larger than the other synandrodes. Male part ellipsoid at the base and tapering towards the apex, circ. 7.5 cm long, yellow. Rhizome cylindrical, armthick.

Distribution: S. Florida, West-Indian Islands, Central America, tropical South America.

Emma Range, above main camp, along creek, alt. 650 m (Daniëls and Jonker 770, fl. July 1959 [U]); id., island in Wosuna fall, alt. 300 m (Daniëls and Jonker 836, fl. Aug. [U]); junction of Paloemeu Riv. and Tapanahoni Riv., marshy creek valley (Wessels Boer 1217, fl. Apr. 1963 [U]).

Vernacular name: Bospomtajer.

6. *Xanthosoma sagittifolia* (L.) Schott
   See Jonker and Jonker in Flora of Suriname I. 2 (1953), p. 53, and the revised description in Notes of the Araceae of Surinam II, Acta Bot. Neerl. 8 (1959), p. 142–143.

Philodendron Schott

1. *Philodendron hederaceum* Schott
   In Notes on the Araceae of Surinam II, Acta Bot. Neerl. 8 (1959),

p. 153 we reported the first record of this species from Surinan. It has since been collected in other parts of Surinam as well.

Perica Riv., near plant. Poelwijk (Splitgerber 813, fl. Apr. 1838 [L]); id., Capoerica ridge (Lindeman 5438, defl. Jan. 1954 [U]); Marowijne Riv., Nassau Mts., alt. 400-550 m (Cowan and Lindeman 39189, fl. Jan. 1955 [NY, U]); Emma Range, IJzermantop, alt. 850 m (Daniëls and Jonker 1107, fl. Sept. 1959 [U]; id. 1110, ster. Sept. 1959 [U]); Zuid Riv., near Lucy Riv. (Schulz and Maguire 10018, fl. July 1963 [BBS, NY, U]); Kabalebo Riv. (Florschütz and Maas 2613, fl. Jan. 1965 [U]).

2. *Philodendron ornatum* Schott

In Notes on the Araceae of Surinam II, Acta Bot. Neerl. 8 (1959), p. 152–153 we reported the first record of this species in Surinam: sterile specimens collected near the bauxite mines at Moengo. The species appeared to be rather common in the Emma Range, both flowering and fruiting specimens were collected. In the granite part of the Emma Range the species occurred both as epiphytes on trees and growing on large boulders. In the dolerite part, however, it was never terrestrial but always epiphytic. For synonymy and description see Notes II, p. 152–153. The dimensions of the leaves in the full-grown, often flowering plants are larger, however, than recorded. The rosulate leaves of the new material reach a length of 60 cm and a width of 45 cm. The denudate part of the posterior ribs is up to 6 cm long. Petiole up to 80 cm.

We are now in a position to give a description of the inflorescence: Spathe up to 22 cm long and 9 cm wide, acute, usually closely convolute but during a short flowering period it opens. The colour of the inner side of the limb varies from yellow to crimson with a white margin; tubular part red inside. Spadix obliquely sessile. Female part cylindrical, 4.5–8.5 cm long and 1.5–2.5 cm in diameter. Ovaries 3- to 6-locular; each locule containing many biseriate ovules. Sterile part of the spadix very short; male part tapering towards the apex, white to cream-coloured, circ. 7.5 cm long and 0.9 cm in diameter. Male flowers consisting of 3–4 anthers which are circ. 1.7 mm long and 1 mm wide. Fruits about 7 mm long and 3 mm in diameter; seeds circ. 1 mm long.

Emma Range, path between camp 15 and main camp, alt. 500 m, on granite rock (Daniëls and Jonker 773, fl. July 1959 [U]; id. 939, fl. Sept. 1959 [U]); id., near South camp, alt. 565 m, epiphytic (Daniëls and Jonker 1121, fl. Nov. 1959 [U]); Cottica Riv., Moengo, forest near bauxite mines (A. M. E. Jonker–Verhoef and F. P. Jonker 484, ster. Jan. 1956 [U]).

3. *Philodendron sphalerum* Schott

Recently collected material from Surinam lead us to the conclusion that we had to unite *P. sphalerum* Schott and *P. longipetiolatum* Engl. The two species were separated before on the base of rather minor characters i.e. length of petioles and leaf blades. The synonymy, a revised description and a list of collections follow.

Philodendron sphalerum Schott, Prodr. Syst. Aroid. (1860), p. 235; Engler in DC., Mon. Phan. Prod. II (1879), p. 373; Engler in Bot. Jahrb. 26 (1899), p. 540; Pulle, Enum. (1906), p. 79; Engler und

Krause in Das Pflanzenreich IV. 23 Db (1913), p. 89; Jonker and Jonker in Acta Bot. Neerl. 2 (1953), p. 74; id. in Flora of Sur. I. 2 (1953), p. 74; id. in Acta Bot. Neerl. 8 (1959), p. 150; – *Philodendron longipetiolatum* Engl. in Bot. Jahrb. 1 (1881), p. 483; Engler in Bot. Jahrb. 26 (1899), p. 540; Engler und Krause in Das Pflanzenreich IV. 23 Db (1913), p. 88; Jonker and Jonker in Acta Bot. Neerl. 2 (1953), p. 360; id. in Flora of Sur. I. 2 (1953), p. 74; id. in Acta Bot. Neerl. 8 (1959), p. 151.

Epiphytic climber. Internodes 2–5 cm long, up to 1 cm in diameter. Leaves entire. Petiole often sulcate in the apical part, vaginate at the base, 10–30 cm long. Leaf blade pergamentaceous, elliptical-lanceolate to triangular-ovate, 10–27 cm long and 4–13 cm wide, acute and cuspidate at the apex, acute, obtuse, rounded or truncate and, usually, more or less cuneate at the base; cusp 1–2.5 cm long; principal lateral veins 4–7 on each side of the midrib, occasionally hardly conspicuous. Sheath 1.5–4.5 cm long. Peduncle 4–9 cm long. Spathe convolute, swollen in the basal half, lanceolate, acuminate, apiculate at the apex, 5–8 cm long, 2–3 cm wide when expanded, outside greenish-white or bright green on the back and light yellow along the margins, inside creamy yellow or white. Spadix shortly stipitate; female part 1.5–2.5 cm long and circ. 2 mm in diameter, light green; sterile part clavate, 0.8 cm long; male part 2–3 cm long, up to 4 mm in diameter, white. Male flowers consisting of 2–3 stamens; stamens prismatic, truncate, circ. 1 mm long and 1 mm wide. Pistils prismatic, circ. 1.5 mm long and 1 mm in diameter; ovary 4- to 6-locular, crowned by a discoid stigma; each locule containing a single, basal ovule.

Distribution: Guiana.

French Guiana (Melinon s.n. [P], type of *P. longepetiolatum* Engl.).

British Guiana, Essequibo Riv. (Jenman 1320 [K]).

Surinam, Lower Suriname Riv., near plant. Kwatta (Kegel 850 [GOET], named by Engler, l.c. (1879), p. 371 and by Pulle, l.c., p. 79: *P. heterophyllum* Poepp.); Suriname Riv., Jodensavanne, Mapane creek, in forest near camp VIII (Lindeman 6720, fl. Dec. 1954 [U]; Schulz 8731, fl. May 1961 [U]); airstrip near Oelemari Riv. (Wessels Boer 1148, fl. March 1963 [U]); Perica Riv., Capoerica ridge (Lindeman 5139, fl. Dec. 1953 [U]); between Left Coppename Riv. and Bakhuis Mts. (Florschütz and Maas 2784 & 2854, fl. Feb. 1965 [U]); without locality (Splitgerber s.n., ex Schott, l.c., type of *P. sphalerum* Schott).

Note: The present authors observed a flowering specimen, Feb. 1956, near Kwakoegron, Lower Saramacca Riv. It was, however, impossible to collect it.

Four other species are new to Surinam, viz.:

4. *Philodendron camposportoanum* G. M. Bar. in Arqu. Jard. Bot. Rio Jan. 14 (1956), p. 269.

Epiphytic on trees and also growing on top of large granite boulders. Petiole terete, up to 43 cm long; the basal 15 cm vaginate. Leaf blade broadly ovate, subcoriaceous, tripartite, light green and prominently veined beneath; midlobe obovate, acuminate at the apex, circ. 33 cm long and 13 cm wide; lateral lobes obliquely ovate to falcate, acute at the apex, up to 24 cm long and 9 cm wide; main ribs of the lateral lobes not denudate. Peduncle 9–15 cm long. Spathe circ. 4.5 cm long and 5 cm wide, shortly cuspidate at the apex, green on both sides. Spadix circ. 5.5 cm long; female part thick-cylindrical to subglobose, circ. 3 cm long and 2 cm in diameter; ovaries 4- to 6-locular; each locule containing numerous, biseriate ovules; male part circ. 2.5 cm long, tapering towards the apex; intermediate sterile part short and inconspicuous. Berries orange-coloured, circ. 5 mm in diameter, arranged in a broad-cylindrical infructescence, crowned by the dried male part and enclosed at its base in a white collar formed by the remains of the spathe.

Distribution: Brazil (Mato Grosso and Amazonas).

Emma Range, E of main camp, path to camp 15, alt. 300 m (Daniëls and Jonker 781, fl. July [U]; Daniëls and Jonker 942, fr. Sept. [U]).

5. *Philodendron tessmannii* K. Krause in Notizblatt 11 (1932), p. 617.

Epiphytic climber on trunks; internodes 2–7 cm long. Petiole long-vaginate; vaginate part 4–7 cm long; apical terete part 0.2-2 cm long. Leaf blade pergamentaceous to coriaceous, elliptical or oblanceolate to obovate, acuminate at the apex and obtuse to cuneate at the base, 10–20 cm long and 3.5–8 cm wide; the two halves slightly unequal. Peduncle 2–4 cm long. Spathe 6–10 cm long; limb up to 2 cm wide, green, mucronate to acuminate. Spadix shortly stipitate; stipe up to 0.5 cm long; female part cylindrical to ovoid, 2–3 cm long and circ. 0.7 cm in diameter, green; male part elongate-conical, 4–5 cm long and 0.7 cm in diameter, greenish white to yellow. Ovaries 3- to 4-locular, 2 mm long and 1 mm in diameter; each locule containing numerous biseriate ovules; stigma discoid. Male flowers consisting of 2 or 3 stamens, circ. 0.6 mm long and 0.5 mm wide.

Distribution: Peru, French Guiana.

Peru: Amazonas, mouth of Rio Santiago (Tessmann 3940, fl. Sept. 1924, isotype [NY]); Junin, near Iquitos (Ellenberg 2967, ster. Sept. 1957 [U]).

French Guiana: Charvein (Benoist 47, fl. Oct. 1913 [P]).

Surinam: Emma Range, E slope of Gonggrijp top, alt. 900 m (Daniëls and Jonker 932, fl. Sept. 1959 [U]); id., South track, alt. 825 m (Daniëls and Jonker 1061, fl. Aug. 1959 [U]).

6. *Philodendron scabrum* K. Krause in A. Engler, Das Pflanzenreich IV. 23 Db (1913), p. 58.

Climber in savannah forest. Stem minutely asperate; internodes 6–14 cm long. Petiole 6–11 cm long; the basal 3 cm vaginate; the upper part verruculose, flattened or slightly canaliculate above. Leaf blade coriaceous, dark green above, lighter beneath, triangular to ovate, cordate at the base, acute and mucronate at the apex, 11–14 cm long and up to 9 cm wide; stronger lateral veins circ. 3 in each half of the leaf blade, hardly distinct from the numerous weaker lateral veins; basal lobes rotundate to obtuse, 3–5 cm long and 2–4 cm wide, their main ribs not denudate in the parabolic sinus, running at a distance of 0.2–0.8 cm from the margin. Peduncle terete, 5.6 cm long. Spathe 6–8 cm long; tube ovoid, dark green outside, crimson inside; limb mucronate, light green on both sides. Spadix obliquely and adnately stipitate; stipe 0.4 cm long; female part light green, circ. 0.9 cm long and 0.6 cm in diameter; male part light red tinged with white, circ. 5 cm long and 0.5 cm in diameter. Pistil circ. 2 mm long and 1 mm in diameter; stigma densely papillose; ovary 6- to 8-locular; each locule containing 6–8 ovules. Male flower consisting of 2–4 stamens, each 1 mm long and 1 mm wide. Inflorescence producing the smell of aniseed. Fruits unknown.

Distribution: Brazil, Amazonas, Rio Branco (once collected, type Ule 8482).

Lobin savannah, between Zanderij I and Hannover (J. & W. A. E. van Donselaar 339, ster. Aug. 1958 [U]); Waneweg, 30 km S of Paramaribo (Kramer and Hekking 2873, fl. Feb. 1961 [U]).

7. **Philodendron polypodioides** Jonk. et Jonk., n. sp. (Fig. 3).

Caulis scandens. Foliorum petiolus teres, circ. 80 cm longus ad 11 cm longitudinis vaginatus. Lamina coriacea, trilobata, triangulata et cordato-sagittata; lobo antico et lobis posticis laciniato-pinnatipartita; laciniae lineares vel interdum bifurcatae nervis principalibus 6. Costae posticae in sinu ad 2 cm denudatae. Pedunculi circ. 3 ex axilla provenientes, 16–18 cm longi. Spatha extus viridis, circ. 14–18 cm longa. Spadix sessilis; pars feminea ad 6.5 cm longa, 1 cm crassa; mascula circ. 5 cm longa. Ovarium circ. 9-loculare; ovula plura, biseriata. Fructus ignotus.

Holotypus: Wessels Boer 1103 in herbario U, e Surinamo ad flumen Oelemari prope portem aëronauticum.

Climber in high forest. Leaves large. Petiole terete, circ. 80 cm long, the basal 11 cm vaginate. Leaf blade subcoriaceous, trilobate, triangular and cordate to sagittate in outline, both the anterior lobe and the posterior ones laciniately pinnatipartite. Anterior lobe circ. 50 cm long and 50 cm wide; posterior ones circ. 40 cm long and 40 cm wide; basal laciniae of the anterior overlapping those of the posterior lobes. Laciniae up to 25 cm long and 1–3 cm wide, ribbon-shaped, gradually tapering towards the subobtuse apex, sometimes bifurcate and occasionally the prongs also bifurcate, provided with up to 6 longitudinal, parallel principal veins. Sinus between the laciniae 1–2.5 cm wide. Midrib of the posterior lobes denudate in the sinus between the posterior lobes; denudate part up to 2 cm long. Circ. 3 inflorescences arising in the leaf axil; peduncles terete, stout, 15–20 cm long. Spathe 14–18 cm long and 2.5 cm in diameter when convolute, mucronate, green outside. Spadix sessile; female part circ. 6.5 cm long and 1 cm in diameter; male part circ. 5 cm long. Pistil circ. 3 mm long and 1.5–2 mm in diameter; stigma capitate, sessile; ovary circ. 9-locular; each locule containing numerous biseriate ovules. Male flowers consisting of circ. 4 stamens. Fruit unknown.

Litani R., Oelemari Riv., near air strip in dry forest (Wessels Boer 1103, fl. March 1963, holotype [U]).

Affinities: This new species belongs in Section *Polytomium* Schott as distinguished by Engler and Krause. It is closely related to *P. fendleri* Krause, an endemic species from Trinidad, which differs, however, in leaf characters.

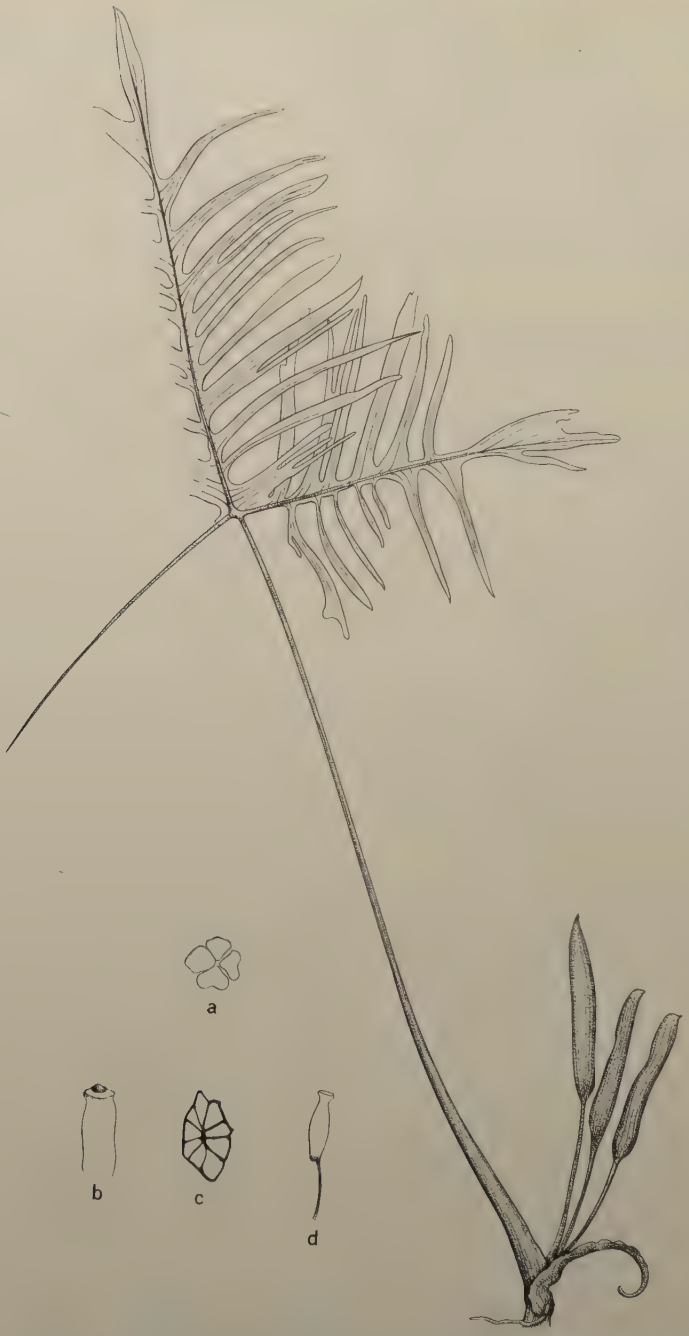

Fig. 3. *Philodendron polypodioides* Jonk. et Jonk. (× 0.15). a. male flower; b. pistil; c. ovary, cross section; d. ovule.

Schismatoglottis Zoll. et Mor.

In Notes on the Araceae of Surinam I (Acta Bot. Neerl. 2 (1953), p. 360–362) the present authors reported the occurrence of a species of the chiefly Malesian genus *Schismatoglottis* in Surinam. The specimens were collected by Maguire on Mt. Tafelberg and described as a new species: *S. americana* Jonk. et Jonk. In the same publication it was suggested that the genus *Philonotion* Schott probably should be sunk in *Schismatoglottis*. Later on more material of *Philonotion* was collected, both in Venezuela and Colombia. It was studied by G. S. Bunting (Annals of the Missouri Botanical Garden 47, 1960, p. 69–71) who, confirming our suggestion considered *Philonotion* a section of the genus *Schismatoglottis*. He regarded *Philonotion williamsii* Steyerm. as a variety of the only other species, *Philonotion spruceanum* Schott, and, consequently, the new section contained two species, viz. *Schismatoglottis spruceana* (Schott) Bunt. and *S. americana* Jonk. et Jonk.

In 1961 Kramer and Hekking collected more material of *S. americana* in the Kappel savannah, S of Mt. Tafelberg. On the basis of the varying leaf shape in this material we were at first inclined to unite *S. americana* and *S. spruceana*. A careful consideration, however, lead us to the conclusion that the two species are distinct and that the newly collected material from Surinam also belongs to *S. americana* of which species a revised description follows here:

Stemless rosulate herb. Cataphylls membranous, lanceolate, acute. Leaves petiolate. Petiole terete, sulcate in the apical part, 8–27 cm long; the basal part vaginate; sheath up to 11 cm long and up to 2 cm wide. Leaf blade thick and fleshy in the living state, in dried material papyraceous to membranous, dark green above and light- to greyish green beneath. On both sides of the midrib 5 or 6 lateral veins, distinct on the back, and between these numerous fine, indistinct lateral veins. On the back of dried leaves minute dots appear in rows between the veins. Leaf blade elliptical to oblanceolate, more or less cuneate to rounded at the base, acuminate and long-subulate at the apex, 10–30 cm long and 2–13 cm wide; the filiform appendix 2.5 cm long, rather stiff. Peduncle 10–24 cm long. Spathe cucullate, subulate at the apex and oblique at the base, 5–7 cm long and circ. 2 cm wide; basal part light green; apical part creamy white; the filiform apical appendage 0.5 cm long. Spadix sessile, adnate in the basal part; the basal female part circ. 1.5 cm long and 0.5 cm in diameter, white; the intermediate sterile part circ. 1 cm long and the apical, male part 2–2.5 cm long, creamy white. Ovary up to 2 mm long and 0.5–1 mm in diameter, cylindrical; placentas 2; ovules few. Stigma annular. Fruit containing 1–3 seeds. Seeds 12-costate, ovoid, apiculate.
Distribution: known from Surinam only.

Tafelberg, northern slope, camp I, about base of waterfalls, alt. 564 m (Maguire 24289, fl. & fr. Aug. 1944 [NY (holotype), U]); Kappel savannah, S foot of Mt Tafelberg, along rivulet, sand stone, alt. 300 m (Kramer and Hekking 2961, fl. Feb. 1961 [U]).

Note: From the above description it appears that the dimensions of the leaves on which Bunting's key was based, are no longer applicable. We distinguish the two species by the consistency of the leaf blades. In the dried specimens of *S. spruceana* the leaf blades are coriaceous, brown above and greyish brown beneath; the lateral veins are all equal and indistinct, not showing the stronger lateral veins and indistinct ones between them as in *S. americana*.

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THE GENERIC NAMES PUBLISHED BY N. M. VON WOLF

R. ROSS

(British Museum (Natural History), London)

(received October 1st, 1965)

O. Schwarz (in Repert. Spec. Nov. Regn. Veg. 47: 288. 1939) was the first in recent years to draw attention to the *Genera Plantarum Vocabulis Characteristicis Definita* of N. M. von Wolf and to the fact that certain generic names were validly published in it for the first time. Mansfeld (in Repert. Spec. Nov. Regn. Veg. 48: 267. 1940; op. cit. 49: 42. 1940) and H. P. Fuchs (in Verh. Naturf. Ges. Basel 72: 344–345. 1961), however, argue that none of the names in Wolf's work can be regarded as validly published. A study of the work and the others associated with it (Wolf, Concordantia Botanica, 1780; Genera et Species Plantarum Vocabulis Characteristicis Definita, 1781) has led me to the opposite conclusion, and in my view some twenty generic names are in fact validly published in Wolf's *Genera.*

Bibliographic details of the works in question are:

Genera Plantarum / Vocabulis Characteristicis / Definita / 1776. [1]–8, table (bound in), [1]–[178]. 8°. There is no indication of author. Pp. 3–177 of the main text are numbered, and on the un-numbered verso of p. 177 there is a list of "Errata".

Concordantia / Botanica. "Nota" on verso of title. 147 pp. innum., sign. A-S 4°, sign. T folio with blank verso to second leaf. Footnote at end of text ([T2] recto) "*Dantisci.* Typo Mülleri & cura N. M. de Wolf. 1780."

Genera et Species / Plantarum / Vocabulis Characteristicis / Definita. / In Marienwerder, / Typis Joan. Jac. Kanteri Typogr. Aulici / 1781. [1]–454 (table pasted in after p. 10) [this is the same table as is bound in after page 8 in the *Genera*], 8 pp. innum. (sign.* "Additamentum Alterum / Sibiricae Cel. Dni. Pallas. / et Aliae Quaedam."), table.

The one copy of the *Genera* that I have seen has the *Concordantia Botanica* bound in behind it, and so had the copies seen by Lampe (Gedachtnissrede auf den Herrn D. Nathanael Mattheus von Wolf in der ausserordentlichen öffentlichen Versammlung der Naturforschenden Gesellschaft zu Danzig am 10. Mai 1785: 29, footnote. 1785) and H. P. Fuchs (in Verhandl. Naturf. Ges. Basel 72: 344. 1961). Because of this Fuchs considers that the *Genera* was not published until 1780, but this does not seem to me to be necessarily so. All copies of the *Genera et Species* with the original title page that I have

seen, and all those for which I have seen an entry in a library catalogue or bibliographic work, have the *Genera* and the *Concordantia* bound in behind them in that order. In those I have seen the preface to the *Genera* is omitted, the first part of the preface to the *Genera et Species* being identical, although partly reset. Lampe (op. cit.: 30, footnote. 1785) says: "Zur Vollständigkeit des ganzen Buches gehören beide Werke, die der Herr *v. Wolf* auch immer, nach gänzlicher Voliendung [sic] beider, zusammen verband; nur ist alsdenn die Einleitung und Tabelle bei den *Gener.* überflussig, weil beides bei den *Gener. & spec.* schon enthalten ist." There is, however, at the British Museum a copy of the *Genera et Species* whose text is printed from the same type as the others but which has a title page reading: *Genera et Species* / *Plantarum* / *Vocabulis Characteristicis* / *Definita.* / Regiomonti / apud Wagner et Dengel / 1782.
and this has neither the *Genera* nor the *Concordantia* bound in, and is also without the "Additamentum Alterum".

It is not possible to elucidate fully the history of the publication of this work on the basis of present evidence, but there is no reason to suppose that, whilst the surviving copies of the *Genera* so far investigated were not issued until 1780 and had the *Concordantia* included, others were not issued earlier. Certainly the *Genera* had been printed before the *Concordantia* was prepared; there are slight differences in the classification adopted in the *Genera* and the *Genera et Species*, and the entries in the *Concordantia* for *Carandas* and *Jasminonerium* correspond to the classification adopted in the *Genera et Species*. There is thus no firm evidence that the *Genera* was not published in the year that appears on its title page, and this should therefore be accepted for the present. It appears that whether the work was published in 1776 or 1780 has no effect on the status of any name as far as priority considerations are concerned, but if the *Concordantia* is treated as part of the *Genera* as originally published *Jasminonerium* is illegitimate (see p. 158 below).

In the *Genera* and *Genera et Species* Wolf sets out a system similar to that in Bergeret's slightly later *Phytonomatotechnie Universelle* (1783–4) by which names for plants are derived from their characters. These names, which we will term formula names, are at three levels, family, genus, and species. The family formula names are of two syllables only and indicate the number of pistils and the number of stamens, whether the stamens are unequal and whether the plants have unisexual flowers, if so distinguishing those that are monoecious from those that are dioecious. The generic formula names indicate the nature and shape of the fruit, the number of seeds, and the shape and number of parts of the corolla, calyx and involucre. The specific formula names indicate whether the plant is woody or herbaceous, annual or perennial, its stature and branching, whether the stems are glabrous or hairy, the shape of the leaves, the type of inflorescence, the colour of the flowers, and the odour or taste of the plant.

The preface to the *Genera* explains this scheme in so far as it deals with family and generic formula names. Wolf uses three letters additional to the normal roman alphabet, a gothic O, a reversed C, and N with an acute accent above. He also distinguishes long vowels from short ones by a circumflex accent over the former. Wolf clearly intended that his formula names should be used in speech as well as writing, for he gives instruction on the pronunciation of the letters. He then sets out how the family and generic formula names are to be formed from the characters of the plants and gives four examples showing how formula generic names are to be formed and how, having done this, one can look in the body of the book and "invenies nomen Scholae: Calligonum", "habebis *Asperula* pro nomine Scholae", "monstrabit Genus: *Solanum*", and "ducit ad *Circaeam*".

The main text of the work is set out in a manner reminiscent of volume 2 of Adanson's *Familles des Plantes*, in that the characters of the genera are given in tabular form. They are divided into un-named classes, sections, and groups of lesser undesignated rank by headings in the text giving their characters, the classes being designated by roman numerals, the sections by arabic numerals, and the lower groups by roman letters, greek letters, and, where further subdivision occurs, by one, two or more asterisks. In the left-hand column the family and generic formula names and the Latin generic names are set out. In the other columns the characteristics of the flower and fruit are given.

In even the lowest subdivisions more than one family formula name often occurs, e.g. on p. 27 under I, 6, a, α, *, there is:

Aî. Saprîri. *Lagoecia.*
Æî. Sæpvîvi. *Eryngium.*

There are even cases where two or more family formula names are associated with the same generic formula name and Latin generic name, e.g. on p. 11:

Æŷ.) Apvævæ.
Æzŷ.) *Andropogon.*

Conversely, the same family formula name can occur in different classes, e.g. on p. 3 under I, 1, b, α, there is:

Aê. Appe. *Parietaria.*

and on p. 57 under II, 3, f, β, there is:

Aê. Bâeve. *Callicarpa.*

There is not a one-for-one correspondence between the generic formula names and the Latin generic names. One Latin generic name can occur as equivalent to more than one generic formula name, e.g. on p. 21:

Azŷ. Apvŷvæ. *Apluda.*

and, in a different group of the lowest rank on the same page:

Azŷ. Apvŷsvæ. *Apluda.*

Often there is an indication of what part of a genus of earlier authors corresponds to a generic formula name, and occasionally which individual species, e.g.:

on p. 93 "Aâ. Wâpamhî. *Delphinium nectario uno.*"
on p. 98 "Yâ. Wŷpamhî. *Delphinium* 3. *Caps. Nect.* 1."
on p. 114 "Yâ. Wŷpæ̂mhî. *Delphinium. Nectariis* 2."

and:

on p. 21 "Æzŷ. Appŷssô. *Hordeum murinum.*"
on p. 24 "Æŷ. Yppŷsnô. *Hordeum.*"

There are some cases where two or more generic formula names are bracketed together as equivalent to one Latin generic name and there is only one entry in the remaining columns against the bracketed formula names, e.g. on p. 6:

		Pist.	*Stam.*	*Semen.*	*Corolla.*
Icî. Apwî.) Apnæ̂.)	*Acnida*	5.	5.	ovatum.	semirot. 5. phyll. & lin. 2 phyll.

Not infrequently there are two Latin generic names cited in connexion with one generic formula name. In many such cases these are the names of a genus of restricted circumscription and that of the larger genus from which it is sometimes segregated, e.g. on p. 128:

Aæ̂. Fâdhemvæ̂. *Bicuculla. Fumaria.*
Aæ̂ Fâphemvæ̂. *Cisticapnos. Fumaria.*
Aæ̂ Fâfhemvæ̂. *Capnoides. Fum.*

In other cases the two names seem to be intended as synonyms, e.g. on p. 8:

Uzû. Upna. *Zostera. Alga.*

and in yet other cases the names seem to be intended as those of independent genera which do not differ in the characters that Wolf used in forming his formula generic names or in his tabulation, e.g. on p. 47:

Aco. Bravo. *Elate*
Cycas
Corypha

At times the same generic formula name, combined with different family formula names, appears in different entries and with different Latin generic names as equivalents, e.g. on p. 47 in addition to the entry cited immediately above there is:

Yco. Bravo. *Phœnix.*

According to the Code, names of genera "may even be composed in an absolutely arbitrary manner " (Art. 20). It follows that where Wolf uses a generic formula name only once and with as its equivalent a Latin generic name not previously validly published, one or other of these two is validly published as a legitimate generic name and the other is published as a synonym. His instructions about pronunciation make it clear that if the generic formula names are regarded as validly published the gothic O should be transcribed as Oi, the reversed C as Sch, and Ń, said to be equivalent to the Spanish ñ, as N. Which of the two types of name is to be regarded as validly published must depend on a decision as to which of them, when there is not a one-for-one correspondence, denotes groups that Wolf regarded as taxa. In considering this point, Wolf's other botanical works need to be taken into account, and when doing so it will be necessary to remember that, in writings of that date, the word "genus" does not necessarily represent a taxon but can have the much wider meaning that it has in the terminology of the Aristotelian philosophy of classification.

The *Concordantia Botanica* is an alphabetical list of plant names, or perhaps it would be better described as two lists combined in one. There are entries in larger type, all of them Latin generic names, that are followed by an indication of the place in Wolf's classification in his *Genera* where the genus is to be found, e.g. "Acer. IV. 5. e. β." The entries in smaller type are followed by an indication of the genus, or in many cases the particular species, of which the name listed is a synonym, species being designated by their number in the third (Vienna, 1764) edition of Linnaeus's *Species Plantarum*. These entries consist not only of Latin generic names and names from classical literature but also vernacular names from German, French and English. There may be a number of entries under one name, e.g.:

Abutilon. Dill. v. *Sida* 12. 15–21. *Malva* 10. 22.
,, Ehr. v. *Napæa*. 2.
,, Plum. v. *Hibiscus*. 11.
,, Sloan. v. *Melochia*. 2. 3.

and in some cases there are both types of entry under one name, e.g.:

Acalypha. III. 1. c.
,, Lin. v. *Tragia* 2.
,, Diosc. v. *Urtica*.

None of Wolf's formula names appear in the *Concordantia*.

When we compare the *Concordantia* with the *Genera*, there are various discrepancies. Some genera that are treated as distinct in the *Genera* are treated as synonyms in the *Concordantia*, e.g. *Bulbine*, and others treated as distinct in the *Genera* are not listed in the *Concordantia*, e.g. *Botryoides*. There are also a number of genera not mentioned in the *Genera* that appear in the *Concordantia* as standing genera with their place in Wolf's classification indicated, e.g.:

Aciphylla. Forst. 1. 6.
Alina. Ad. III. 6. a. α.
Amerimnon. Br. IV. 5. c. δ.

The *Genera et Species Plantarum Vocabulis Characteristicis Definita* has a preface of which the first part is identical with that of the *Genera*, although partly reset, and which continues with an account of the way in which specific formula names are to be formed. Its main text consists of entries in which the following are set out:

Family formula name,
Generic formula name,
Latin generic name or names,
Specific formula names preceded by a figure indicating the number of the species in the third (Vienna, 1764) edition of Linnaeus's *Species Plantarum*. Occasionally the Latin epithet of the species is added, especially when it is a generic name in apposition.

There are symbols indicating the continents from which plants come. These follow the Latin generic name when they apply to all species of the genus, otherwise they follow some or all of the specific formula names.

When two Latin generic names appear in an entry, one is a name not used by Linnaeus in the third edition of the *Species Plantarum* and the other is the generic name under which the species cited are placed by Linnaeus in that work. Occasionally there are three Latin generic names, two being synonyms for a genus not recognized by Linnaeus and the third that of the genus in which Linnaeus included it, e.g. on p. 101: "*Bustia. Asteroid. Buphthalmum.*"

The arrangement of the *Genera et Species* is the same as that of the *Genera* as far as the classes and sections of that work are concerned. The divisions immediately below the level of section are also, for the most part, the same in the two works, but below this level the classification is different, grouping being on habit in the *Genera et Species* and on floral characters in the *Genera*.

Although there are in the *Genera et Species* some specific formula names not preceded by the number of the species in the third edition of the Linnaeus's *Species Plantarum*, there is at least one species from that work cited in almost every generic entry, and genera not considered at all by Linnaeus are almost all omitted, even if they were included in the *Genera*. Thus in Classis I, the only genus in the *Genera et Species* under which no species from the *Species Plantarum* is cited is *Condea*. There are also a few cases where a species number has been omitted as a result of a manifest error, e.g. on p. 59:

Æŷ. Jcvîvæ. *Arundo. Bambos.* Ropavî.

In the same class in the *Genera* there are, however, the following, none mentioned in the *Genera et Species*:

Ancistrum Forst.
Ascarina Forst.
Gahnia Forst.
Laxmannia Forst.
Pennantia Forst.
Schawia Forst.
Tardaval
Thryocephalum Forst.

The authorities above are as given by Wolf; *Tardaval* was published by Adanson.

Following the main body of the work there is an *Index Linnaei*, each entry of which consists of a Latin generic name, a generic formula name, and a list of species giving both their number in the third edition of the *Species Plantarum* and their Latin epithet, and the page where their specific formula name is given. There is only one generic formula name given for each genus, even where there are more both in the *Genera* and in the main body of the *Genera et Species*, e.g. on p. 18 of the *Genera* there is:

Aî. Epvivi.) *Echium.*
Ephivi.)

and on pp. 51–53 of the *Genera et Species*:

Aî. Ephivi. *Echium.* 1) . . . .
Aî. Epvivi. *Echium aequale.* 2) . . . . 3) . . . .
Aî. Ephivi. *Echium inaeq.* 4) . . . . 6) . . . . 7) . . . .
Aî. Ephivi. *Echium.* 5) . . . .

but in the *Index Linnaei*, p. 384:

Echium. Epvivi. 1) – 7) . . . .

with no mention of Ephivi.

Following the *Index Linnaei*, there is a page of errata, including the following two entries:

transfer. Tamarindus ad paginam 295. lin. 3.

dele *totum genus Balsamine, et transfer.* ad pag. 298. in lineam 15.

This is followed by four pages of addenda and six of examples of how specific formula names are formed, the left-hand column having entries of this type:

Rqbarbæd.
Fagus sylvestr.

Finally there is an *Additamentum Alterum Sibiricae Cel. Dni. Pallas, et aliae quaedam*, with entries in this form:

pag. lin.
14 16 Æzê. Ynvy. Ribarze. *Betula fruticosa.*

The evidence in favour of the view that it is the Latin names and not the formula names that denote taxa seems to me to be overwhelming. The various points can be summarized thus:

Different family formula names occur in the same groups of the classification adopted, and are even bracketed together in connexion with the same generic formula name, and the same family formula name occurs in widely different parts of the classification. This shows that they do not denote taxa.

Generic formula names are bracketed together and associated with a single Latin generic name and a single set of tabulated characters. Where more than one Latin generic name is associated with a single generic formula name, the Latin names are never bracketed together.

The equivalents in the *Concordantia* for names treated there as synonyms are Latin generic names, not generic formula names.

In the errata to the *Genera et Species* entries in the main text are referred to by their Latin generic names and not their generic formula names.

The formula names must therefore be regarded not as names of taxa but as mnemonics for artificial groups, those denoted by generic formula names being more or less equivalent to taxonomic genera.

In consequence, any Latin generic names in the *Genera* that were not previously validly published and that are the only ones in a particular entry must be regarded as validly published by Wolf, for he gives diagnostic details. Where there is more than one Latin generic name in an entry, none can be regarded as validly published, for even in the case where one is that of a segregate genus corresponding to the generic formula name and the other that of the wider genus in which it was included by, e.g., Linnaeus, the status of the smaller taxon is uncertain. Wolf may well have regarded it not as a genus but as a subdivision of one.

If this view is rejected, then all Wolf's generic formula names must be regarded as validly published generic names. They cannot be rejected on the basis argued by Mansfeld (in Repert. Spec. Nov. Regn. Veget. 49: 42. 1940) that they are two-word names, the family formula name being part of the generic name, even although the same generic formula name is used in connexion with different family formula names for different taxa. Wolf in his preface (p. 6) definitely states that the single-word generic formula name is "generis nom[en]", and such cases as *Bravo* (see p. 150 above) and *Wêêwe*, cited by Mansfeld, would have to be regarded as the simultaneous publication of homonyms.

Fuchs apparently had not seen the *Genera et Species* when he wrote: "N. M. von Wolf beabsichtigte, wie aus dem ganzen Werk hervorgeht, eine monominale Nomenklatur technische Art einzufuhren", nor had he adequately studied Wolf's preface when he termed the generic formula name *Fæ̂pcvira*, which he misspells "Fâepcvirs", "unaussprechbar" (in Verhandl. Naturf. Ges. Basel 72: 345. 1961). The generic formula names cannot be rejected on these grounds, but only for the reason that it is the Latin generic names and not the formula names that represent taxa.

The following is an annotated list of the generic names first published in Wolf's *Genera*:

Archangelica Wolf, Gen. Pl. Vocab Char. Def.: 32 (1776).
Type: *Angelica atropurpurea* L.
cf. Wolf, Gen. & Sp. Pl. Vocab. Char. Def.: 75 (1781).

Wolf in his *Genera* uses this name for a genus with "umbella rubra", but does not maintain it in his *Genera et Species*; against the same generic formula name under the heading "umbella rubra" in that work he has the entry:

Angelica. 3) Wypîrdfû.
This is *Angelica atropurpurea* L.

Wolf's use of this name antedates that by Hoffmann (Gen. Pl. Umbell. 1: 161. 1814), for a genus consisting of *Archangelica officinalis* Hoffm. (= *Angelica archangelica* L.) and *A. atropurpurea* (L.) Hoffm. These species are nowadays normally retained in *Angelica.*

Botryoides Wolf, Gen. Pl. Vocab. Char. Def.: 83 (1776).
includes: *Hyacinthus comosus* L.
H. botryoides L.
H. racemosus L.
cf. Wolf, Gen. & Sp. Pl. Vocab. Char. Def.: 173 (1781).

H. botryoides L. should presumably be taken as the type of this genus. It is a taxonomic synonym of *Muscari* Mill., which Wolf treats as a separate genus including *Hyacinthus muscari* L. and *H. monstrosus* L. (cf. Wolf, Gen. & Sp. Pl. Vocab. Char. Def.: 173. 1781).

Bulbine Wolf, Gen. Pl. Vocab. Char. Def.: 84 (1776).
includes: *Anthericum aloöides* L.
A. annuum L.
A. asphodeloides L.
A. frutescens L.
A. hispidum L.
cf. Wolf, Gen. & Sp. Pl. Vocab. Char. Def.: 171, 175 (1781).

In the present list of conserved names, *Bulbine* Willd. (Enum. Pl. Hort. Berol.: 372. 1809. type: *B. frutescens* (L.) Willd.) is conserved against *Bulbine* J. Gaertn. (Fruct. 1: 41. 1788). This conservation is unnecessary, but because of it *Anthericum frutescens* must be taken as the type of *Bulbine* Wolf. The list of conserved names needs to be suitably amended.

Carthamoides Wolf, Gen. Pl. Vocab. Char. Def.: 39 (1776).
includes: *Carduus acanthoides* L.
Carduus altissimus L.
Carthamus carduncellus L.
Carthamus coeruleus L.
Carthamus creticus L.
Centaurea alpina L.
Centaurea centaurium L.
Cnicus acarna L.
cf. Wolf, Gen. & Sp. Pl. Vocab. Char Def.: 95, 97, 98 (1781).

It is somewhat difficult to be sure that Wolf intended to indicate the species of *Carduus* and *Centaurea* listed above as belonging to this genus, but this seems to be so. The species listed are currently referred to the following genera, all published before 1776: *Carduus* L., *Carduncellus* Adans., *Carthamus* L., *Centaurea* L., and *Cnicus* L.

Catunaregam Wolf, Gen. Pl. Vocab. Char. Def.: 75 (1776).

This generic name was used by Adanson (Fam. Pl. 2: 85, 534. 1763) but was not validly published by him as he spelled it as two words "Catu Naregam". It is based on the "Katou-Naregam" of Rheede (Hort. Malab. 4: 29, t. 13. 1683), whose identity is uncertain but which is probably either *Randia uliginosa* (Retz.) Poir. or *R. brandisii* Gamble.

G. Taylor (in Exell. Cat. Vasc. Pl. S. Tomé: 197. 1944) drew attention to the fact that *Randia* L. *sensu lat.* was highly heterogeneous and Keay (in Bull. Jard. Bot. Brux. 28: 15 et seq. 1958), in a revision of the West African species previously referred to *Randia* and *Gardenia* Ellis, came to the conclusion that *Randia*, the type of which is an American species, was not represented in Africa. In a revision of the Asiatic members of this alliance, *Catunaregam* Wolf will require to be taken into consideration and may prove to be the correct name for one of the segregate genera, possibly that now known as *Xeromphis* Raf.

Cervaria Wolf, Gen. Pl. Vocab. Char. Def.: 28 (1776).
includes: *Anthamanta cervaria* L., which clearly should be taken as type, and one other species.
cf. Wolf, Gen. & Sp. Pl. Vocab. Char. Def.: 74 (1781).

This is a taxonomic synonym of *Peucedanum* L. This publication antedates that of Gaertner (Fruct. 1: 90. 1788), hitherto regarded as the first publication of this name. It is an earlier homonym of *Cervaria* L. (Amoen. Acad., ed. 3, 1: 415. 1787, *nom. superfl.*), a name which Linnaeus never intended to publish as a substitute for *Ortegia* Loefl. ex L.; he had used it in an early dissertation reprinted in 1787, but had dropped it before 1753.

Coralloides Wolf, Gen. Pl. Vocab. Char. Def.: 174 (1776).
includes: *Lichen fragilis* L.
L. paschalis L.
L. rangiferinus L.
L. rocella L.
L. subulatus L.
cf. Wolf, Gen. & Sp. Pl. Vocab. Char. Def.: 345 (1781).

In the *Concordantia* (E 2 verso), Wolf has the entry "Cladona Br. v. *Coralloides Lichen*". It is therefore clear, as his diagnostic matter in the *Genera* strongly suggests, that he was using this name in the sense of *Cladona* P. Browne ex Adans. One of the species that he includes in the genus in the *Genera et Species* is *Lichen subulatus* L., the type of *Cladonia* Wiggers, *nom. cons.* This species should clearly be taken as the lectotype of *Coralloides* and that name added as *nomen rejiciendum* versus *Cladonia* in the Code.

Publication of this generic name is normally attributed to Hoffmann (Descr. Adumbr. Pl. Lich. 2: 25, t. 31 fig. 2. 1791), but he gave no generic description, only a description of a previously known species, *Lichen globiferus* L., which he refers to the genus.

Eragrostis Wolf, Gen. Pl. Vocab. Char. Def.: 23 (1776).
includes: *Briza eragrostis* L.
Poa eragrostis L.
cf. Wolf, Gen. & Sp Pl. Vocab. Char. Def.: 63, 65 (1781).

This publication antedates that of Palisot de Beauvois (Essai Nouv. Agrost.: 70. 1812), usually taken as the first publication of this name, although it has sometimes been attributed to Host (Ic. & Descr. Gram. Austr. 4: 14. 1809), who, however, provided no generic description. This publication by Wolf means that the names *Eragrostis major* Host (loc. cit) and *Eragrostis minor* Host (tom. cit.: 15) are validly published names, and the example in Art. 43 of the Code should be deleted. Since Palisot de Beauvois (op. cit.: 74. 1812) removed *Briza eragrostis* to his new genus *Megastachya*, *Poa eragrostis* (*Eragrostis minor*) must be taken as the type of *Eragrostis* Wolf.

Jasminonerium Wolf, Gen. Pl. Vocab. Char. Def.: 57 (1776).

The name "Jasmino-nerium" was first used by Linnaeus in his *Flora Zeylanica* (:191. 1747), where he included it in the "Obscurae Pentandria" and quoted one synonym from Plunkenet and another from Hermann and Burmann. He appears never to have cited "Jasmino-nerium" nor either of these synonyms in any subsequent work. Adanson (Fam. Pl. 2: 171, 532, 564. 1763) treats "Jasmino-nerium" of Linnaeus as a synonym of his genus *Carandas* (based on "Carandas Rumph., Herb. Amboin. Auct.: 57, t. 25. 1755), on which Linnaeus also based his genus *Carissa* (Mant. Pl. 1: 7. 1767), with originally the single species *C. carandas* L. (tom. cit.: 52. 1767). *Carissa* L. is conserved against *Carandas* Adans.

In his *Genera* Wolf does not mention *Carandas* or *Carissa*, but in the *Concordantia* he has the following entries:

"Carandas. Rump. II. 3. d." in large type indicating a standing name (D 1 verso).

"Jasminonerium. Lin. v. *Karandas*." (I 4 verso).

and in the *Genera et Species* (:132. 1781):

"*Jasminonerium. Carandas. Nerium.* 4) Reldavwa."

In both the *Genera* (p. 129) and the *Genera et Species* (p. 267) Wolf treats *Nerium* as a separate genus, placing it among the plants whose fruit is a siliqua, whilst *Jasminonerium* is placed among those whose fruit is a bacca. Under *Nerium* in the *Genera et Species* there is also a "4) Reldavwa" listed. *Nerium* no. 4 in the third edition of the *Species Plantarum* is *N. zeylonicum* L., now known as *Wrightia zeylonica* (L.) R. Br.

In this confusing situation it would seem correct to conclude that *Jasminonerium* Wolf in his *Genera* is based on the "Jasmino-nerium" of Linnaeus, which in its turn is based on a specimen in Hermann's herbarium (vol. 3, fol. 24, specimen numbered "405" by Linnaeus, 405 being the number of "Jasmino-nerium" in the *Flora Zeylanica*). This specimen has been identified by Trimen (Hand-b. Fl. Ceyl. 3: 125. 1895) as *Carissa spinarum* L., and there seems no reason to suppose that this identification is incorrect. Wolf then, between 1776 and 1780, came to agree with Adanson that his *Carandas* and Linnaeus's "Jasmino-nerium" were synonyms. At the generic level this is correct and *Jasminonerium* Wolf is a synonym of *Carissa* L., *nom. cons.*; if Wolf's *Genera* and *Concordantia* are regarded as a single work, *Jasminonerium* is illegitimate, being a superfluous substitute for *Carandas* Adans., *nom. rejic.*, and *Carissa* L., *nom. cons.*, but, as already pointed out (p. 148), I consider this view incorrect.

Wolf's entries in his *Genera et Species* presumably indicate that he thought that two separate species were included under *Nerium zeylonicum* in the third edition of Linnaeus's *Species Plantarum* (:306. 1764), one that now known as *Wrightia zeylonica* (L.) R. Br. and the other that now known *Carissa carandas* L., in which species he included the "Jasmino-nerium" of Linnaeus.

In the *Genera et Species* Wolf uses a different basis of classification into third-order subdivisions within his section II. 3. from that adopted in the *Genera*. In this latter the entry for *Jasminonerium* is in under II. 3. f. *β*., whereas in the *Genera et Species* the entry for the genus is under II. 3. d.; the entry in the *Concordantia* for *Carandas* corresponds to that in the later work. This is one of the reasons for considering that the *Genera* was originally published separately from the *Concordantia*.

Karekandel Wolf, Gen. Pl. Vocab. Char Def.: 73 (1776).

This is based on the "Kare-Kandel" of Rheede (Hort. Malab. 5: 25, t. 13. 1685), which is a species of *Carallia* Roxb., *nom. cons.* It was formerly listed as a *nomen rejiciendum* versus *Carallia*, being attributed to Adanson (Fam. Pl. 2: 88, 532. 1763) but has been deleted from the most recent edition (1961) of the Code because, as correctly pointed out by Rickett and Stafleu (in Taxon 9: 69. 1960), Adanson spelled it as two separate words "Kare Kandel" and hence did not give it valid publication. It must now be reinstated in the list but attributed to Wolf.

Martagon Wolf, Gen. Pl. Vocab. Char. Def.: 84 (1776).
includes: *Lilium chalcedonicum* L.
L. martagon L.
L. pomponium L.
L. superbum L.
cf. Wolf, Gen. & Sp. Pl. Vocab. Char. Def.: 174, 175 (1781).

This is a taxonomic synonym of *Lilium* L. It is usually cited as having been published by Salisbury (Gen. Pl.: 57. 1866). *L. martagon* L. should obviously be regarded as the type species.

Mutellina Wolf, Gen. Pl. Vocab. Char. Def.: 31 (1776).
Type: *Phellandrium mutellina* L.
cf. Wolf, Gen. & Sp. Pl. Vocab. Char. Def.: 77 (1781).

This is a taxonomic synonym of *Ligusticum* L. No other post-Linnaean author seems to have used this generic name.

Myrthoides Wolf, Gen. Pl. Vocab. Char. Def.: 73 (1776).
Type: *Myrtus caryophyllata* L.

Wolf (Gen. & Sp. Pl. Vocab. Char. Def.: 156. 1781) has the entry "*Myrthoides. Myrthus.* 1) Ridapvan *", but in the same work (op. cit.: 158. 1781) he has "*Myrthus.* 1) Ripdapza. Ridabza. Ridavza. *vulg.* 3) . . . ." He distinguishes *Myrthoides* from *Myrtus* primarily of on the basis that the former has "Semina solitaria. Sem. 1" and the latter "Semina plura in locis aliquot. loca 3." From this it would appear that the "1)" in the *Myrthoides* entry is an error for "11)", designating *Myrtus caryophyllatus* L., and that that is the type of *Myrthoides*; this is accordingly a taxonomic synonym of *Syzygium* Gaertn. (Fruct. Sem. Pl. 1: 166. 1788), *nom. cons.*, and should be added to the list of names rejected against it.

Napellus Wolf, Gen. Pl. Vocab. Char. Def.: 114 (1776).
includes: *Aconitum lycoctonum* L.
A. napellus L.
A. pyrenaicum L.
A. uncinatum L.
A. variegatum L.
cf. Wolf, Gen. & Sp. Pl. Vocab. Char. Def.: 240 (1781).

Wolf separates *Napellus* from *Aconitum* L. in his *Genera*, restricting *Aconitum* to those species with a quinque-partite gynoecium, viz.: *A. anthora* L. and *A. cammarum* L. In the *Genera* & *Species*, however, he does not treat *Napellus* as a separate genus. As Linnaeus's original description of *Aconitum* (Gen. Pl., ed. 5: 236. 1754) includes "Pist. *Germina* tria (quinque) . . . . . Obs. Anthora *Pistillis quinque instruitur*", his name must be typified by a species with a tripartite gynoecium, and *A. lycoctonum* is usually recognized as the type of the genus. *A. napellus* should presumably be taken as the type of *Napellus*. All the species that Wolf included in *Napellus* are currently retained in *Aconitum*; even if that genus were to be divided along the lines suggested by Wolf, that name would have to be retained for the segregate he calls *Napellus*. However, as Wolf neither cites synonyms nor lists included species in his *Genera*, *Napellus* cannot be treated as a *nomen superfluum*.

Napellus is usually attributed to Fourreau (in Ann. Soc. Linn. Lyon, nouv. ser., 16: 327. 1868), who raised to generic rank *Aconitum* sect. *Napellus* DC. (Regn. Veg. Syst. Nat. 1: 371. 1817). As this section includes the type species of *Aconitum*, *Napellus* has been considered a *nomen superfluum*. The entry for this name in the *Index Nominum Genericorum* requires correction.

Olusatrum Wolf, Gen. Pl. Vocab. Char. Def.: 30 (1776).
includes: *Smyrnium integerrimum* L.
S. olusatrum L.
cf. Wolf, Gen. & Sp. Pl. Vocab. Char. Def.: 74 (1781).

Smyrnium olusatrum should clearly be taken as the type of this genus. This species is normally regarded as the type of *Smyrnium* L., which Wolf treated as distinct, and hence *Olusatrum* cannot be regarded as a superfluous name. *Smyrnium integerrimum* is currently placed in *Taenidia* Drude. I cannot trace that any author since Linnaeus other than Wolf has used *Olusatrum* as a generic name.

Phalaroides Wolf, Gen. Pl. Vocab. Char. Def.: 11 (1776).
includes: *Phalaris aquatica* L.
P. arundinacea L.
P. phleoides L.
cf. Wolf, Gen. & Sp. Pl. Vocab. Char. Def.: 34, 36, 38 (1781).

Phalaris phleoides L. is currently placed in the genus *Phleum* L. and the other two species are normally retained in *Phalaris* L. I cannot trace that any other author than Wolf has used *Phalaroides* as a generic name.

Pinea Wolf, Gen. Pl. Vocab. Char. Def.: 156 (1776).
includes: *Pinus cembra* L.
P. pinea L.
cf. Wolf, Gen. & Sp. Pl. Vocab. Char. Def.: 316 (1781).

This is a taxonomic synonym of *Pinus* L., and *Pinus pinea* should clearly be regarded as its type. I cannot find that any other author has separated these two species from that genus.

Spelta Wolf, Gen. Pl. Vocab. Char. Def.: 22 (1776).
Type: *Triticum spelta* L.
cf. Wolf, Gen. & Sp. Pl. Vocab. Char. Def.: 61 (1781).

This is a taxonomic synonym of *Triticum* L. No other author that I can trace has used this generic name since 1753.

Vaccaria Wolf, Gen. Pl. Vocab. Char. Def.: 111 (1776).
includes: *Saponaria cretica* L.
S. vaccaria L.
cf. Wolf, Gen. & Sp. Pl. Vocab. Char. Def.: 234 (1781).

Saponaria vaccaria is clearly to be taken as the type of this name. The genus is currently recognized as distinct (cf. Dandy, List Brit. Vasc. Pl.: 26. 1958. – Chater in Tutin *et al.*, Fl. Europ. 1: 186. 1964) and valid publication of its name is usually attributed to Medikus (Phil. Bot. 1: 96. 1789), who did not, however, provide any validating matter. Recently it has been thought that its first publication was by Moench (Meth. Pl. Hort. Bot. Agri Marburg.: 63. 1794) and that the name of its type species was in consequence *Vaccaria parviflora* Moench (loc. cit.) (cf. Index Nom. Gen.: no. 10/14856). The fact that the generic name was validly published by Wolf means that *Vaccaria pyramidata* Med. is the correct name for the type species.

The entry for this genus in the *Index Nominum Genericorum* requires correction.

Vincetoxicum Wolf, Gen. Pl. Vocab. Char. Def.: 130 (1776).
Type: *Asclepias vincetoxicum* L.
cf. Wolf, Gen. & Sp. Pl. Vocab. Char. Def.: 269 (1781).

The question of the correct name for the genus typified by *Asclepias vincetoxicum* L. has recently been discussed by H. P. Fuchs (in Verh. Naturf. Ges. Basel 72: 343 *et seq.* 1961) and a full synonymy is given by him. His conclusions, however, are based on the view that the latin generic names published by Wolf are published in synonymy, but this, as is argued above, is erroneous. The correct name of the genus is therefore *Vincetoxicum* and of its type species *V. hirundinaria* Med. (in Hist. Comment. Acad. Elect. Theod. Palat. Mannheim, Phys. 6: 404. 1790). Walter (Fl. Caroliniana: 104. 1788) must be considered to have given a new description of an already published genus and to have referred two new species to it; Walter provides descriptions for all genera mentioned in his work, whether they had been published previously or not.

The entry for this genus in the *Index Nominum Genericorum* requires correction.

Zeocriton Wolf, Gen. Pl. Vocab. Char. Def.: 21 (1776).
includes: *Hordeum distichon* L.
H. zeocriton L.
cf. Wolf, Gen. & Sp. Pl. Vocab. Char. Def.: 59, 444 (1781).

This generic name is normally attributed to Palisot de Beauvois (Essai Nouv. Agrost.: 114. 1812). *Hordeum zeocriton* should clearly be regarded as its type. It is currently regarded as a taxonomic synonym of *Hordeum*.

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THE EARLY EVOLUTION OF THE ARCHEGONIATAE: A RE-APPRAISAL

A. D. J. MEEUSE

(*Hugo de Vries Laboratory, University of Amsterdam*)

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Abstract

After a re-appraisal of the alternative hypotheses concerning the origin and the early evolution of the archegoniate land plants, the postulation of a thalassiophytic group of precursors with free isomorphic alternating generations by Church, Zimmermann, and several others is rejected. Several versions and modifications of this 'homologous' theory, such as Fritsch's suggestion of diminutive filamentous algal being the progenitors of the vascular plants and Jeffrey's idea of an advent of partly emerged (aerial) sporangiate extensions of an aquatic sporophyte, are equally untenable. In the present author's opinion the old and reputedly almost obsolete 'antithetic' theory is much more compatible with the relevant evidence, provided this hypothesis is more precisely formulated. The conquest of the land must have begun with the gradual migration of the *gametophytic* (haploid) generation to semi-terrestrial or temporarily dry habitats *before* the development of a vegetative diploid phase. The first stage after the colonisation of semi-terrestrial and subsequently of terrestrial environments by presumably still prostrate life forms consisting of filamentous algal strands must have been the differentiation of a portion of this haploid type into a more massive parenchymatous soma which remained prostrate in many cases and bore the sessile sporangia. In bryophytes such differentiations of the gametophyte may themselves be more or less erect and thus raise the sporangia into an undeniably aerial position (as in many Musci), or they produce upright extensions on which the gametangia are produced and, later on, the sporangia are inserted (as in *Marchantiales*). Ontogenetically the phylogenetic sequence is frequently recapitulated in that first a filamentous protonema develops from a germinated spore and only afterwards a more important gametophytic structure (typically developed in the *Bryales*). In other instances the sporangium is, or was, not supported and 'lifted' into the air by a part of the haploid plant but by an *intercalated* sporangial stalk (sporangiophore) which is a vegetative diploid structure and constitutes the modest beginning of the large sporophytes of the Higher Cormophyta. The intercalated vegetative diploid structure originated subaerially and was *ab initio* a terrestrial organism, i.e., the sporophyte did not develop out of a submerse aquatic archetype by a process of adaptation as is assumed in the 'homologous' theory. The vegetative sporophyte and, accordingly, the characteristic features of the terrestrial plants such as the vascular (stelic) tissues, on the contrary developed *de novo* and the sporangiophore is consequently *sui generis* in respect of both the gametophytic and the sporangium (representing the phylogenetically older portions of the plant). The *Anthocerotales* are reminiscent of this early evolutionary level of the Hemitracheophyta which must *ab initio* have had, or soon acquired, green and partly independent (photo-autotrophic) sporophytes. The phylogenetic history of the *Bryophyta* and of the *Hemitrachyophyta* is discussed in the light of the new interpretation of the subaerial transmigration Certain pertinent problems of evolution (mono- or polyrheithry) and of homology (morphological equivalence of certain structures versus inhomology through independent, i.e., *sui generis*, origin) are tentatively analysed. These considerations have an important bearing on our views concerning the relationships of various archegoniate groups and reveal flaws in several 'established' ideas some of which concern certain aspects of the Telome Theory.

1. THE ALTERNATIVE HYPOTHESES

Some recent summaries dealing with the origin of the early terrestrial plants (e.g., CHRISTENSEN, 1954, 1957; ZIMMERMAN, 1955, 1959, 1965; ANDREWS, 1960a; AXELROD, 1959; STEWART, 1960, 1964) suggest that the three principal points of inquiry are (1) the "transition" from a non-tracheophytic (or at least a non-archegoniate) precursory phase to the proper terrestrial plants, (2) a monophyletic descent starting from a single group of telomic or pre-telomic organisms resembling the *Psilophytales* (or perhaps the *Anthocerotales*), or a polyrheithric development, and (3) the advent of the first truly tracheophytic forms, which is almost certainly of pre-Devonian, but according to some exaggerated claims even of Cambrian age. In my opinion, the first question is by far the most pertinent, because the possible answers to the other two depend to a large extent on the acceptance of the mode of origin of the terrestrial sporophyte. It is this topic that still needs exhaustive treatment, because there are some controversial issues which are not so apparent, most workers suggesting in their writings that the so-called homologous theory has completely superseded the older "antithetic" hypothesis (see, in addition to the above-cited authors, e.g., TAKHTAJAN, 1953; STEINBÖCK, 1954, 1959; PROSKAUER, 1960). The majority of them accept the so-called thalassiophytic origin of the archegoniate forms, *in extenso* developed by CHURCH (1919), which theory requires the postulation of a group of putative progenitors of the terrestrial plants, the Thalassiophyta, which are supposed to have been rather large marine algae with isomorphic alternating generations (i.e., with a free-living, well-developed sporophyte). Strong adherents of this idea of a descent of the archegoniate plants from such large marine ancestral types are, apart from Zimmermann, e.g., STEWART (1964) and CORNER (1964). Some dissident opinions were expressed by FRITSCH (e.g., 1945) who pointed out, among other things, that, instead of larger precursors invading the land, the possibility of diminutive algal forms migrating to the terrestrial habitat deserves serious consideration. However, he left the question open whether a migration from the sea or from the fresh water must be accepted as the more likely event, although he himself was inclined to postulate the conquest of the land by intertidal marine forms. VISCHER (1953) agrees with Fritsch's ideas in many respects, but decidedly favours fresh water forms as the putative progenitors of the archegoniate plants. CHRISTENSEN (1954) brought a very fundamental point to the fore: irrespective of the primary origin of the archegoniate plants from aquatic organisms with isomorphic generations, the question must be considered whether the originally free-living sporophyte had already become dependent ("parasitic") on the gametophyte (and at the same time had become reduced) before or after subaerial transmigration. Zimmermann and several other authors evade the issue, but, as CHRISTENSEN (1957) re-emphasized, this aspect of the hypothesis of the homologous alternating generations has a considerable bearing on the relative position of the Bryophyta (and especially so of the *Anthocerotales*) in respect of both the earliest land plants and the various pteridophytic forms. The bryophytic sporophyte may be "reduced" or "advanced" as compared to a common ancestral form of pteridophytes ("tracheophytes") and bryophytes (PROSKAUER, 1960). Such ideas did not change the main theme of the theory, the advent, at some time or another, of a progenitor of the cormophytic plants with isomorphic generations.

The alternative theory, presupposing the alternation of "antithetic" generations, or, in Zimmermann's terminology, the intercalation of a sporophytic generation between the gametophytic ones, is older and goes back to Hofmeister. If one would only go by the opinions expressed by such authorities as Zimmermann, Corner, and several others, the antithetic theory is entirely obsolete.

Indeed, since the publications by WETTSTEIN (1935) and by CAMPBELL (whose last paper on the subject appeared in 1940), no other botanist seems to have seriously challenged the homologous theory (or "transformation theory" as Zimmermann has it) postulating progenitors with alternation of isomorphic generations. Even JEFFREY (1962), who has pointed out that "*the question of the evolution of land plants is primarily a biological one, of which the evolution of water economies comprises a major part*", and that this question has been largely ignored in most discussions of the problem, surprisingly still adheres to the idea of isomorphic diplohaplonts being the progenitors of the archegoniatae (although he assumes that the sporophyte develops from the fertilised egg cell *in situ* and is borne on the gametophyte). The present publication, apart from being a compilation of the more recent opinions on the subject, is a re-consideration of exactly these ecological aspects of the evolution of the *Archegoniatae*. The corollary of the ensuing deductions is a plea for the rehabilitation of the old theory of antithetic generations, albeit on somewhat different grounds than those on which the theory was originally conceived by Hofmeister and other protagonists of the "intercalation" theory.

2. SOME FUNDAMENTAL CONSIDERATIONS

As mentioned previously, Christensen and Jeffrey pointed out certain facets of the problem of proto-cormophyte evolution which had not previously been extensively treated in most of the relevant publications. In spite of CHRISTENSEN'S (1957) most pertinent statement that this aspect was neglected by ZIMMERMANN (1955), the latter (1959, 1965) did not reconsider the possibility of the conquest of the land by a form with the sporophytic generation ("already") dependent on the gametophyte at the time of sporulation, instead of by some "*Urlandpflanze*" in which the originally isomorphic *gametophyte* had become reduced in size in respect of the sporophyte (see, e.g., ZIMMERMANN, 1955, p. 300, fig. 3; 1959, p. 130, fig. 56 B; 1965, p. 21, fig. 6, and p. 46, fig. 16). This is the crux of the whole problem of the origin of the archegoniate plants, because irrespective of the early history of their still completely aquatic progenitors, their first terrestrial precursors were according to Christensen's interpretation no longer plants with isomorphic alternating generations. Similarly, JEFFREY's (1962) idea of a partial emergence of the originally submerse sporophyte and an increase in size of the subaerial sporangium-bearing portion is an important emendation of CHURCH's original views. There are several other basic assumptions on which the "homologous" theory rests that are not at all convincing and can certainly be challenged. In the first place, the habitat of the putative algal ancestors: was it the marine intertidal zone or the fresh water? The arguments adduced by Jeffrey certainly point to the second alternative. The hypothetical thalassiophytic progenitors are consistently described as fairly large to large green seaweeds, but according to ideas developed by FRITSCH as early as 1916 (and re-published in extenso in 1945) there are several direct and indirect indications pleading in favour of the postulation of small to diminutive prostrate algae living in fresh water (or even on wet ground) being the ancestral forms. JEFFREY (1962) uses the same reasoning (without citing Fritsch's papers) and submitted some relevant ecological evidence. These considerations have a considerable bearing on the most probable evolutionary sequence of events: did the two generations of the plant (gametophyte and sporophyte) both attain their maximum development *before* the conquest of the land (followed by the retrograde development of one of them), or did only one of them do so? The *Thalassiophyta* were "modelled" after the highest forms of marine algae (including the predominantly marine *Phaeophyta* and *Rhodophyta*) with a massive parenchymatous soma, but the putative ancestors of all land plants must have been green algae on biochemical and phytochemical grounds, so that neither the structure nor the life-cycles of the other algal groups can possibly have any bearing on the problem under discussion. The evidence provided by the recent green algae is anything but convincing and in point of fact the origin of the land flora must indeed rather be sought among the diminutive green, and still filamentous, oogamous forms of the fresh water or moist soils (VISCHER, 1953). Intimately linked with this deduction is the question of the relative development of the two generations. As I pointed out before, Church and most of the other adherents of the hypothesis of the alternation of isomorphic generations in the thalassiophytic archetypes of the Archegoniatae imagine free-living and mutually independent haplontic and diplontic phases (see, e.g., Zimmermann's figures already quoted in this chapter). However, as Fritsch pointed out, there are no recent green algae that could adequately fit the part required by the thalassiophytic theory. Fossil remains of algal forms cannot have any demonstrative force in this connexion because we can only in exceptional cases ascertain the true taxonomic position of these fossils, i.e., whether they were red, brown, or green algae.

The postulation of an alternation of free isomorphic generations of algal precursors in the transformation hypothesis implies that both phases were originally autotrophous plants with practically the same ecological requirements, which in turn requires the assumption that the gametophyte and the sporophyte migrated simultaneously to the terrestrial environment, or approximately so. None of the recent archegoniate land plants has a completely submerse-aquatic phase combined with a terrestrial alternating generation! However, whereas the sporophyte, in the train of thought of the "homologous" theory, "acquired" the characteristic features of the terrestrial plants (a cuticle, stomatic openings, vascular, or stelic, tissues, non-motile cutinised spores), the gametophyte did nothing of the sort and even became reduced instead. It was exactly this moot point which incited CHRISTENSEN's emendation of the theory and Jeffrey's version of the conquest of the land, the first author explicitly stating (1957) that the common ancestor of the *Bryophyta* and the *Pteridophyta* had a sporophyte which was parasitic on the gametophyte, and the second postulating and initial association of the two phases, the submerged sporophyte forming subaerial sporangiate outgrowths. In all these reconsiderations the sequence of events (the time factor) is of paramount importance. If we start from the plausible assumption that the haploid phase of the generation cycle was the first to develop a vegetative soma of an appreciable size, the diploid phase lagging behind in this respect, many speculations can be simplified or even rendered superfluous by considering the possibility of a migration of the gametophytic plant to the terrestrial habitat *before* the development of a sporophyte of an appreciable size. This amounts to the re-instatement of the intercalation theory, of the hypothesis of antithetic alternating phases, *in optima forma*, as we shall see, and this requires some comment.

3. WHEN DID THE TRANSMIGRATION FROM WATER TO LAND TAKE PLACE?

After the first multicellular green algae had evolved, which must have happened a very long time ago in an aquatic environment, even the early filamentous and perhaps still planktonic forms must gradually have filled other ecological niches: the intertidal marine environment, the fresh water, and subsequently also, via temporarily flooded ground, moist terrestrial habitats. It is very likely that the conquest of the land started from such habitats as shallow freshwater pools drying out periodically. Even to this day algal froms with a primitive organisation, i.e., filamentous form with a hardly developed diploid phase, are by no means rare in semi-terrestrial situations and on dry land (VISCHER, 1953). There are, therefore, no arguments precluding an early adaptation of primitive filamentous forms to a truly terrestrial life. This has already been emphasised by Fritsch, Vischer, Jeffrey, and others, but this simple and logical starting point of our inquiry into the origin of the land flora has up to now been obscured by the assumption that a vegetative sporophyte of at least modest dimensions had developed *before* the gametophytic generation had become completely terrestrial or approximately so. Jeffrey has summed up the ecological and physiological evidence for his contention that a truly terrestrial plant is fundamentally different from a submerse aquatic form in several respects. As Jeffrey rightly says (l.c., p. 449): "Direct colonisation of the land by littoral intertidal algae seems quite improbable". The gradual "adaptive" evolution of terrestrial forms is explained by Jeffrey by postulating that a portion of a submerse sporophyte was, so to speak, gradually raised above the water and assumed the characteristics of the terrestrial sporophyte as it became more important by producing additional vegetative soma. In view of the evidence from recent (semi-)terestrial green algae and pteridophytic prothalli I cannot visualise a migration as suggested by Fritsch, Jeffrey (or Christensen for that matter) for the very same reason, viz., the different physiology and ecology of submerse aquatics and of land plants. The crux of the problem can be expressed by the question why, as suggested in the older hypotheses, the *gametophyte* was induced by some selective evolutionary force to leave the medium to which it was best adapted after it was accompanied by a vegetative sporophyte. It is much more logical to suppose that the whole development of the vegetative sporophyte took place subsequent to the migration of the gametophyte to a (semi-)terrestrial environment. As Jeffrey has rightly emphasised, the selective advantage of an aerial diaspore dispersal becomes apparent in perodically changing habitats (monsoon pools, and the like), but this applies to haplontic forms as well as to diplonts, in other words, the advent of the non-motile cutinized spore was not necessarily coupled with the presence of a vegetative sporophyte of appreciable dimensions.

If we take this as the starting point of our deductions and postulate that the colonisation of the land by algae started at the phylogenetic level of a still insignificant diploid phase, the gametophytic generation of the terrestrial algal ancestors of the archegoniate plants must have been a plant of a modest to diminutive stature, most probable consisting of prostrate filaments. The protonemata of the mosses are strongly reminiscent of this early evolutionary phase, in my opinion. Sexual reproduction of these early forms was perhaps rather primitive, as in e.g., Charophyta, but at some time or other the already sessile oocyte must have been retained on the gametophyte to develop into a sessile sporangium. It is rather irrelevant in this connexion whether at this stage the spores were already non-motile or still of the ciliate zoospore type, and if the prostrate filaments had either already evolved into a prostrate frondose (thallose) soma, or became differentiated into prostrate and more or less erect portions (the latter bearing the archegonia and later the sporangia). The sequence is not so important, but at some time or other there must have been prostrate thallose haploid forms with sessile sporangia, or prostrate gametophytes with erect archegonium-bearing portions which raised, as it were, the sporangia into the air. It is already at this early phylogenetic stage that the first divergent evolution must have taken place which is conceivably still reflected in the morphology of the gametophytes and the sporophytes of the various groups of the Bryophyta at the present-day level. In several cases the erect and more

Salient points	'Homologous' theory (CHURCH, ZIMMERMANN, etc.)	Do. emende 1945;
Suggested progenitors of terrestrial plants.	Marine algae of intertidal zone with alternation of independent isomorphic generations; haploid and diploid phases (fairly) large, evolution monophyletic; this hypothetical group referred to as 'Thalassiophyta'.	Aquatic to t tous) heterot with isom gametophyte to diminutiv (subaerial) monophyleti
Development of gametophyte and sporophyte at the beginning of the conquest of the land.	The gametophyte is supposed to have become reduced before or soon after the adoption of a terrestrial way of life; the sporophyte must have become adapted to a subaerial existence and developed vascular tissues etc. de novo or from a pre-vascular cell differentiation in precursory algal forms.	Do.
Morphology of early subaerial sporophyte.	Very similar to thalassiophytic prototype, but with adaptations to terrestrial existence (cuticle, stomata, stele).	Do.
Evidence from fossils.	No unequivocal records of Thalassiophyta; Eocormophytes are already too diversified to be of decisive importance in any objective judgment of the hypothesis.	Do.
Evidence from recent forms.	Large Chlorophyceae with free-living isomorphic generations and reproducing by means of oogamy unknown, i.e., recent forms fitting the part of the Thalassiophyta are non-existent.	Small heter with erect are known, eration us tions not is ed in the th
Adaptation and ecological requirements.	Migration of large marine sporophyte to the land and adaptation to terrestrial life is postulated.	Do. (but o algae not p
Position of the Bryophyta.	Bryophytes are supposed to be reduction lines, the gametophytes predominating and the sporophyte having undergone a retrograde development and secondarily dependent on the gametophyte; Anthocerotales not necessarily primitive.	It seems p phyta have lutionary (FRITSCH, generation come seco the gameto

6,	Do. emended by JEFFREY, 1962	'Antithetic' or 'intercalation' theory, present author's version
- e s; e t n	Aquatic filamentous green algae showing a homologous alternation of generations but sporophyte developing directly from zygote and attached to gametophyte, phases of modest size; sporophyte initially submerse but developing aerial portions emerging from the water which bear the sporangia; evolution of early stages monophyletic.	Subterrestrial to terrestrial prostrate filamentous algae, with only a haploid vegetative phase which bore the sessile sporangia; the haploid plant of a modest size; early evolution presumably monophyletic.
	Gametophyte initially not very much reduced; development of large sporophytic generation after the thallus portion supporting the sporangia had emerged from the water.	No vegetative diploid phase (which developed only after the gametophyte had colonised the terrestrial habitat); reduction of gametophyte only started after a vegetative sporophyte of an appreciable size had originated.
	Only a portion emerging from the water becoming a true terrestrial organism (and later predominating).	Originating as an intercalated sporangial stalk (sporangiophore) which gradually increased in size and which was from the very beginning of its existence adapted to a life in a terrestrial environment.
	Do.	Fossils such as Sporogonites suggest an early type of prostrate terrestrial plant with solitary stalked sporangia, which renders a thalassiophytic origin most unlikely.
ns s' n- a- t-	All the evidence points to small heterotrichous algal progenitors occurring in fresh water, the sporophyte developing on gametophyte after oogamy, but in recent forms no isomorphic sporophyte.	Small heterotrichous filamentous algae without a substantial asexual (diploid) generation not infrequently found in (semi-)terrestrial habitats are suggestive of putative progenitors.
er	Ecological requirements and other considerations render the migration and adaptation of large sea weeds altogether inconceivable.	Do., but for the same reasons migration and adaptation of large submerse fresh water sporophytes is not very probable either.
o- o- wn ual e- on	Bryophytes, but more particularly the Anthocerotales, are still rather close to early archegoniate land plants.	Do.

aerial differentiations of the gametophyte became rather elaborate structures bearing the gametangia (and subsequently the sporangia), the sporangia remaining sessile on the gametophyte, as in *Marchantiales* and several groups of the Musci (but not in the *Bryales*). The second evolutionary trend was the development of a diploid sporangial stalk which was virtually intercalated between sporangium and gametophyte. The most pertinent examples of such plants are the fossil taxa *Sporogonites* (as reconstructed by ANDREWS, 1960b) and *Eogaspesiea* (DABER, 1960) of Devonian age, but also the *Anthocerotales* are not far removed from this type of plant. The bryophytes with a stalked sporangium, mainly found among the *Bryales*, show both trends, *viz.*, the development of an intercalated sporangiophore and the differentiation of the gametophyte into a prostrate early phase (the protonema) and a (frequently erect) secondary phase producing the gametangia (and later bearing the sporangiophores). The position of the *Anthocerotales* is indubitably somewhere near the crossroads of the phylogenetic lines of the bryophytes and the tracheophytes, but we should not be too rash in identifying them with progenitors of the vascular plants, because the gametophyte has presumably already become reduced in size and importance in respect of its ancestral form, which we must imagine as a flat organism, either consisting of a dense meshwork of protonema-like filaments, or thallose in structure and resembling a large hornwort gametophyte, but with sessile sporangia.

4. SOME CONSEQUENCES OF AN EARLY CONQUEST OF THE TERRESTRIAL HABITAT

The most important consequence of the postulation of an early migration of the haploid generation before the intercalary development of a vegetative sporophyte between gametophyte and sporangium is that the formed sporangiophores originated *de novo*, so that one does not have to assume an "adaptation" of an originally aquatic (or even submerged!)sporophyte to a new environment. The gametophyte remained a low prostrate plant of modest size and retained some of the characteristics of an aquatic, the proximity of the substratum apparently providing sufficient moisture, but the intercalated vegetative sporophyte developed (indeed "antithetically"!) as a terrestrial organism right from the beginning. Jeffrey's objection to a change-over from a submerse way of life (or something very similar to it in semiterrestrial habitats) to a truly subaerial existence is thus satisfactorily met with: some characteristic physiological and morphological features of the sporophyte originated *ab initio* and not as a secondary adaptation to a "new" habitat.

Another topic brought up by the last-mentioned author is the possible early association of the haplontic algal form or the primitive gametophyte with fungi. In this case I think not only his deductions are basically sound, but also the reconstruction of the phylogenetic history is quite plausible. In lichens the fungal component appears to be the dominant partner (being the only one capable of sexual reproduction), but in many terrestrial orchids the mycorrhizal hyphae are virtually "milked" and there can be very little doubt about the predominance of the orchid. One can easily visualise an alternative evolution of an initial (and more or less incidental or "loose") association of fungi and, still haplontic, semiterrestrial algae, viz., the development of a mycorrhizal relation between the two in which the algal component, though predominating, became more and more dependent on the fungal partner by the loss of its original photosynthetic capacities. The development of the mycotrophic prothalli of several pteridophytic groups can thus be satisfactorily explained, and also the fact that they became more massive and frequently subterraneous, perhaps even acquired an increased longevity. However, this was a secondary development which apparently did not occur, or had not yet initiated, in the evolutionary lines leading, eventually, to the recent bryophytes, most of the true ferns, and the water ferns. A certain amount of polyphyletic or polyrheithric evolution must have taken place which will be discussed presently. An important conclusion is that if MERKER (1958, 1959) is right in his identification of the rhyniaceous subterranean organ (the so-called "rhizome" in the previously current terminology) as the long-lived gametophytic generation, it is doubtful whether *Rhynia* and its closest allies can be regarded as representing ancestral forms of other tracheophytic groups with green, non-mycotrophic prothalli. I shall return to these points presently when various phylogenetic aspects will be considered.

As regards the physiology of the intercalated vegetative sporophyte, there are again alternative possibilities. If one starts from the assumption that it primarily only developed as the result of selective processes favouring spore dispersal by raising the sporangium as far as possible above the frequently moist and hence unfavourable substratum, it was completely dependent on the gametophyte and presumably did not possess assimilatory plastids, but almost certainly developed a cuticle. The transport of substances supplied by, or via, the gametophyte and translocated in a watery medium (as solutes or in colloidal solution) must soon have necessitated adequate means of providing an upward flow of water, evaporation providing the translocation mechanism; in other words, stomata originated. In addition the support of the sporangia presumably induced the advent of a structural strengthening device, the central xylem strand so characteristic of the stele of early telomatic cormophytes. The other possibility is that the sporophyte became a green and partly self-supporting structure at a very early stage. Both conditions are neatly illustrated by the *Bryophyta*: in such groups as the *Bryales* the sporangiophore is completely "parasitic" on the gametophyte, whereas in the *Anthocerotales* a photosynthetic sporangiophore is found. In my opinion it is not a foregone conclusion that the sporophytes of all archegoniate plants are strictly homologous in the sense that the sporangiophore of the *Bryales* is a derivative of a partly autotrophous vegetative sporophyte of a type still found in the *Anthocerotales* (or *vice versa*).

Obviously, only a sporophyte provided with chloroplasts could eventually become the predominating phase of the two alternating generations. If the development of the large sporophytes of the pteridophytes and the spermatophytes was indeed an evolutionary process that took its origin in a vegetative diploid growth of modest size,the homology of these large sporophytes rests upon a common origin from a very simple structure, the intercalated diploid sporangiophore. Differences in the stelic structure, and in the mode of branching and the development of some characteristic morphological and anatomical features in the various pteridophytic groups need not necessarily be explained as semophyletic differentiations of the same basic structural pattern provided by a common group of isotomously bifurcating telomic progenitors resembling the sporophytes of the *Rhyniaceae*. There must have been enough room for the evolution of convergent and of parallel trends, whilst some fundamental differences persisted (compare also the arguments adduced by AXELROD, 1959). The suggested new working hypothesis concerning the origin of the sporophytes of the terrestrial plants manifestly has a considerable bearing on the inquiry into early Archegoniate evolution, and on the phylogeny of and the relationships among the Bryophyta in particular. Some of the relevant points have been tabulated in the accompanying Table I (see pages 168, 169) in which various theories are compared.

5. IMPLICATIONS OF THE MOST LIKELY SEQUENCE OF EVOLUTIONARY PROCESSES AND TRENDS

It appears to be reasonably well established that the migration of filamentous and oogamous green algae from the fresh water habitat to damp soils started at a very early phase in the phylogeny of algal groups. This can be visualised as a gradual change-over from a submerse life to a sessile life on periodically flooded soils, followed by a progressive adaptation to a truly "terrestrial", drier habitat. These ancestral algal forms developed a sporangium and a more massive haplontic soma. The sporangium produced soon, if not *ab initio*, cutinised spores. The more parenchymatous gametophyte may have developed from suberect aerial differentiations arising from the prostrate filaments as found in recent heterotrichous algal forms. The more massive haploid phase must have been semiprostrate in many cases, but may have been erect (as in many of the true mosses or *Musci*) or formed erect differentiations (as in *Marchantiales*), thus "raising" the sporangium into the air, the medium favouring the release and the dispersal of the dry, air-borne, and cutinised spores. It is doubtful whether in the precursors of the vascular plants the gametophytes formed erect aerial protrusions of an appreciable size, the sporangia being supported by newly intercalated sporangiophores. This may have been preceded, or followed, by an association of the gametophytic algal form with a fungus to form a mycotrophic prothallus. The sporangial stalk may or may not have been partly photo-autotrophic, but ultimately possessed a cuticle, stomata, chloroplasts, and stelic tissues. The advent of the specialised conductive tissues will be discussed presently in connexion whit the evolution of the *Bryophyta*. The primitive vegetative sporophytes or sporangiophores were completely dependent on the gametophytes at least as far as their mineral nutrition is concerned. A fairly massive prostrate gametophyte, as found in the thallose Hepatics and *Anthocerotales*, and, like the latter, bearing a number of erect sporangiophores, may well represent the ancestral type of the tracheophytes. Such archicormophytes, accordingly, had a morphology which agrees in many respects with that of the fossil form genus *Sporogonites* and of the recent hornworts. This is a far cry from the postulation of dichotomously branched sporophytes of the *Rhynia* type as the first terrestrial plants in the Telome Theory (Zimmermann's "*Urlandpflanzen*", supposed to have inherited their extensive soma and dichotomous mode of branching from a thalassiophytic, i.e., completely submerged, diploid algal archetype). The question of a strictly monophyletic or a polyrrheitric descent of the principal groups of the Cormophytes, discussed by AXELROD (1959), among others, must be answered by assuming that their common progenitors had approximately the morphology of a *Sporogonites* and that from this archetype divergent evolutionary lines emerged. This has some far-reaching implications, in the first place with regard to the Telome Theory: not all major pteridophytic taxa went necessarily through a psilophytalean (rhyniaceous) level of organisation, so that, for instance, they need not have acquired the same morphological type of "leaf" and may have developed either "enation leaves" (Lyco-leaves) or "megaphylls". Similarly, the mode of branching, the stelar anatomy, and also the mycotrophic or autonomous gametophyte evolved independently in several parallel lineages. There may have been some "retrograde" steps in the Bryophyta, the gametophyte becoming even more important than was the case before. Upon the whole the reduction of the gametophyte advanced rapidly, but although it became reduced to modest dimensions, the early ontogenetic stages of the sporophyte are still dependent on it at least for supplying the necessary mineral nutrients (and, of course, water).

Another consequence of such a phylogenetic sequence is that there is no fundamental homology between the gametophyte, the sporangium, and the sporangiophore (a *de novo* intercalated vegetative sporophyte). These parts had an independent origin and can be considered to be *sui generis* in respect of each other. One of the arguments seemingly pleading against this antithetic nature of the originally aquatic gametophyte and the *ab initio* terrestrial sporophyte, recently mentioned again by ZIMMERMANN (1965), is the occasional occurrence of tracheids in the prothallia of *Psilotum*. This phenomenon has no demonstrative force, because there are several other examples of neotenic and proterogenic "shifts" of characteristics of post-ontogenetic developmental stages, a well-known and neatly comparable example of characters "spilling over" being the occurrence of tracheids with the characteristics of tracheary elements of the secondary xylem in the metaxylem of some dicotyledonous woody plants. The "adult" feature is "brought forward", as it were, to an earlier ontogenetic stage. This is a matter of genetic potencies and the changed time of appearance of the phenotypic expression of the genetically determined (and initially dormant) feature. A similar explanation can be given to account for the advent of the green photo-autotrophous sporangiophore: the organism had a potential genetic constellation responsible for the synthesis of assimilatory pigments in plastids in certain cells and these determining factors only expressed themselves in the gametophyte, but not necessarily in the newly formed vegetative sporophyte. A "shift" of the expression of these potencies (latently present in the genome of the nuclei of the sporophyte as well as in the gametophyte) to the sporophyte was all that was needed to start the evolution of the large and secondarily independent (photo-autotrophic) sporophyte of all higher *Cormophyta*.

Finally, one more aspect of the suggested early evolution of the vascular plants must be considered. The advent of the sporophyte as an intercalated stalk-like structure necessitates the assumption that the dichotomously branched psilophytalean forms, which were after all the archetypes of at least some (though not necessarily of all) groups of pteridophytic and progymnospermous plants, developed out of the somewhat less complex and solitary sporangiophores. The well-known fact that the sporophytes of all eotracheophytes bore several to numerous sporangia suggests that the dichotomously branched telomic *Urlandpflanze* of Zimmermann's Telome Theory, a plant with the morphology of a *Rhynia* or a *Horneophyton*, actually represents an aggregate of a number of stalked sporangia, an association of a number of elementary green rod-like sporophytes (sporangiophores) bearing terminal sporangia. The gametophytes of *Sporogonites*, *Anthoceros*, and several bryophytes (e.g., Bryales) each produce or produced a number of individually stalked sporangia. A reduction in size of the gametophytic soma automatically resulted in a closing of the ranks of the sporangiophores and it is feasible that they became partly fused, the coalescence phylogenetically starting at the base and proceeding acropetally. The individual sporangiophores became "tufted" or "fascicled" by apparently emerging from a common base. A more or less staggered fusion of such bunches, combined with an ontogenetic "back-shift" of the commencement of the elongation of the fused basal portions of the sporangiophores, would result in the formation of a repeated branching system and of mesomes, respectively. This stage calls to mind the Lower Devonian fossils described as *Eogaspesiea* and *Hicklingia*, whose decidedly "tufted" appearance and somewhat irregular (instead of strictly isotomous) bifurcations are, in my opinion, strongly suggestive of this mode of origin. The acropetal fusion of telomic sporangiophores must in certain cases have initiated the more complete lateral fusion of the sporangium-bearing elements which resulted in the formation of sorial and synangial complexes. This trend originated early, witness the morphology of such forms as *Hedeia*, *Yarravia*, *Zosterophyllum*, and *Horneophyton*, and soon became manifest in the *Primofilices* and *Progymnospermopsida* with soral or synangial aggreates of sporangia. However, this general trend of aggregation of sporangiophores need not always have resulted in the morphological pattern of the psilophytic plants. It is feasible that in fundamentally the same way the verticillate mode of branching of the Sphenophyta originated and also the polysporangiate fertile axes of the *Lycophyta*. The possible connexion between the longitudinal fusion of protostelic sporangiophores and the stelar structure of the stems of *Sphenophyta* and *Lycophyta* (with several protoxylem strands) may form a future point of inquiry, even if only leading to interesting speculations. In any event one must postulate an early divergent evolution of the vascular plants starting from a primitive phylogenetic level of the sporophyte, in other words, a polyrheitric descent from ancient land plants (architracheophytes), rather than a more monophyletic development from psilophytalean prototypes as envisaged in Zimmermann's Telome Theory.

6. THE RELATIONSHIPS AND POSITION OF THE BRYOPHYTA

Although the organisation of the bryophytes did not change fundamentally from that of an earlier terrestrial precursor, the fossil remains of the first unmistakable representatives are not known from strata older than the Lower Carboniferous. This could be interpreted as indicative of a relatively late origin of this group, but there are several plausible explanations to account for their late arrival on the scene. In the homologous (transformation) theory (see, e.g., HASKELL, 1949; STEINBÖCK, 1954, 1959) the *Bryophyta* are considered to be reduced forms evolved as the result of a retrograde development of the sporophyte from an ancestral form with isomorphous generations, i.e., from a thalassiophyte or an *Urlandpflanze* in the sense of ZIMMERMANN (e.g., 1959, p. 130, fig. 6, reproduced in ZIMMERMANN 1965, p. 21, fig. 6). This has even taken the form of the postulation of a reduction of the sporophyte to the extent of an almost complete loss of the stelic structure that was supposed to be present in the progenitors; see, e.g., PROSKAUER'S (1960) discussion of the occasional occurrence of columellar cells with helical cell wall thickenings among the *Anthocerotales*. This implies that the ancestral forms of the *Bryophyta* would either not be recognised as such among the fossil records or only be preserved in the form of the reduced sporophytic phase, and of sporangia (and spores), which would not unequivocally point to a bryophytic nature of these remains. In this train of thought the differentation of the originally very delicate and perhaps ephemerous gametophyte into a more massive structure took place rather late and only enabled the recognition of the fossil bryophytes a fairly long time after their evolution had begun. In the alternative intercalation theory the same arguments are relevant, but in a somewhat different context. The evolution of the group was perhaps mainly "progressive" instead of "retrograde" in that the ancestral terrestrial forms consisting of a low prostrate thallus with sessile sporangia developed into a much more massive gametophyte organism showing special adaptations and differentiations in the mosses and hepatics, with the exception of the *Anthocerotales* in which the sporophyte became relatively more important. I am not in favour of an explanation of bryophyte evolution as a "reduction" of an anthocerotalean form for two reasons. In the first place, the sporangia are sessile in the Hepatics and in the mosses, the *Bryales* excepted, and even in the *Bryales* the vegetative sporophyte (sporangiophore) is hardly autonomous. If we admit that the sporangial stalks of the *Bryales* are not necessarily derived from those of the hornworts but may have originated as a parallelism, I believe that a more logical explanation of the early phylogeny of all bryophytes is the postulation of an ancestral form with a fairly massive prostrate gametophyte as in *Sporogonites*, but bearing sessile sporangia. The intercalation of a sporangial stalk by a diploid growth, followed by a reduction of the gametophyte resulted in a phylogenetic line leading to both *Anthocerotales* and Hemitracheophyta. The intercalation of a more or less erect outgrowth of the gametophyte (a gametangiophore) between the prostrate gametophytic soma and the sporangium may have produced a phylogenetic line culminating in the true mosses and liverworts. The *Anthocerotales* are still very close to the *Hemitracheophyta* but they did not develop much beyond the evolutionary level of the progenitors common to both. It is possible that the anthocerotalean *sporophyte* is somewhat reduced in respect of this ancestral group, if the latter already possessed differentiated stelic tissues (tracheidal elements and the like). This is of course altogether conjectural, and that is why I believe that PROSKAUER's (1960) deductions concerning the possible nature and origin of the elongated cells with helical ("spiral") cell wall thickenings which he discovered in the sporangial columella of a few representatives of the hornwort family can also be "reversed". His conclusion that the elater-like cells of the columella are modified (reduced) tracheidal elements which underwent a partial transference of function (namely from a purely water-conducting capacity in the columella and the sporophytic sporangial stalk to a partial spore-dispersing function) can equally well be reversed by assuming that, before there was any vegetative sporophytic soma, elater cells were involved in the opening mechanism of the sporangia and/or spore dispersal which had already developed a reinforced cell wall and thus acquired the capacity to accumulate, and conduct, water. The intercalation of the vegetative sporophyte favoured every evolutionary trend to shift the limits of occurrence of these water-accumulating elements towards the columella and eventually farther down into the sporangiophore. This would, among other things, be compatible with the central position of the xylem in the oldest type of stelic structure, the protostele, and with the development of conductive elements in the sporophyte alone (the exceptions, some prothalli of *Psilotum*, need not refute the general validity of this rule as we have seen). The position of the Anthocerotales, then, is most probably that of an archaic group still exhibiting features of the earliest land plants which were the common ancestors of the *Anthocerotales* and other *Bryophyta*, the *Psilophyta*, and the remaining groups of the *Cormophyta*. Similarity in morphological, anatomical and embryological features between *Anthocerotales* and, e.g., *Bryales*, *Sphagnales*, *Andreaeales*, *Hepaticae* and *Psilotales*, supports the postulation of their common origin, but does not necessarily indicate a closer relationship between the hornworts and, e.g., the mosses, than exists between *Anthoceros* and *Psilotum*, or between *Musci* and *Hepaticae*.

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LACTICIFEROUS PLANTS OF THE KARAPARANÁ-IGARAPARANÁ REGION OF COLOMBIA

RICHARD EVANS SCHULTES
(Botanical Museum of Harvard University)

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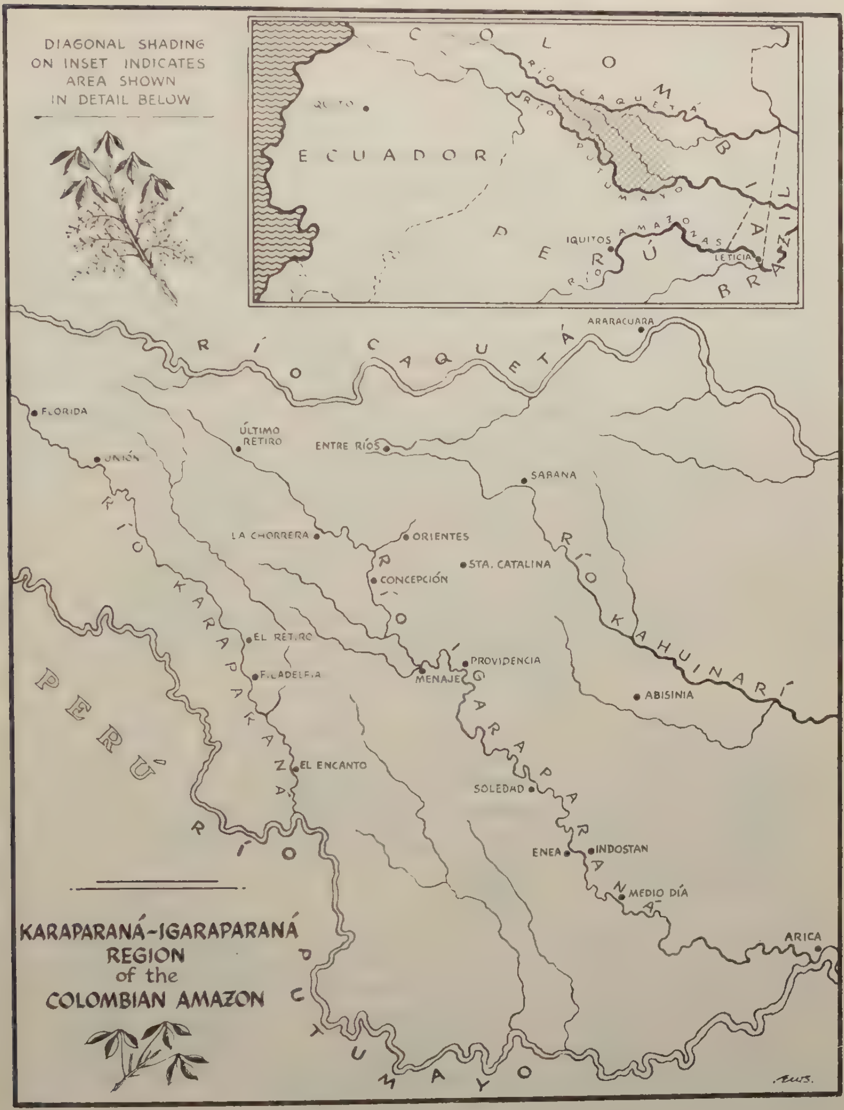
During the first fifteen years of the present century, the production of rubber from wild trees was a thriving, though nefarious, industry in the northwestern part of the Amazon Valley. The heaviest concentration of this primitive forest industry — and the most widely notorious — was centered in the area drained by the Ríos Karaparaná and Igaraparaná, northern tributaries of the Río Putumayo, lying between the Ríos Putumayo and Caquetá (Map 1).

In this hey day of rubber production, the area was claimed by both Colombia and Peru, but the Peruvians actually occupied and exploited it. As a result of the war between Colombia and Peru in the early 1930's, the boundaries have been set with the Río Putumayo as the frontier. Colombia is now in possession of the areas north of the Putumayo, which are incorporated into the Colombian political unit known as the Comisaría del Amazonas.

Historically, the "Putumayo", as this former rubber-producing area is known, holds great importance, if only because of the uncontrolled and inhuman atrocities committed on defenceless and peaceful Indian inhabitants by agents of the rubber company (Peruvian Amazon Company). As a result of mistreatment, disease and malnutrition, a decrease of the native population from an estimated 40 000 or 50 000 to about 10 000 during the first decade of the century took place. These troubled times and the region and its geography have been very thoroughly reported in W. E. HARDENBURG: "The Putumayo — the devil's paradise" (1912), T. WHIFFEN: "The north-west Amazons" (1915) and P. SINGLETON-GATES and M. GIRODIAS: "The black diaries of Roger Casement" (1959) 201–315.

Botanically, this region holds great importance, insofar as rubber is concerned, because of the kinds of trees that were exploited. The rubber produced here fell far short of being a product of high quality, but tons of it did enter world commerce, and specimens from the source trees have occupied, at times, the critical attention of taxonomists and economic botanists. Indeed, new species of *Hevea* have been based on several collections made in the area.

During the course of taxonomic studies of *Hevea* and its close ally *Micrandra* and the preparation of a paper on minor rubber plants of Colombia, I have had to take into historical and botanical account specimens and information relating to the so-called "Putumayo" rub-



Map 1.

ber boom of the early years of this century. I have tried to interpret some of the data in the light of field experience gained in this area in 1942. Supplementary to certain data in the literature, herbarium specimens and documents preserved at the Royal Botanic Gardens, Kew, have been most helpful. I wish to acknowledge the kindness of the authorities at Kew who, during my visits there in 1947 and 1950, and, most recently, in May, 1964, have placed their wealth of material at my disposition.

We have a rather complete collection of specimens from the region of the Karaparaná-Igaraparaná made by Mr. Walter Fox in 1910. Interesting notes on these collections were published in the Kew Bulletin of Miscellaneous Information for 1912 (1912) 74. Although the merciless exploitation and barbarous treatment of the natives were carried out by local employees of the Peruvian Amazon Company, much of the company's capital was British. As news of the atrocities, ever more alarming, leaked out and found its way to London, British representatives were sent over to these remote Amazon forests to investigate the working and living conditions of the native rubber tappers. Fox, former Superintendent of the Botanic Garden in Penang, Malaya, was one of these commissioners. He was not a taxonomic botanist, but he rendered science a unique service in collecting botanical material of the sundry lacticiferous trees under exploitation in this part of the Amazon by the Company and in making significant botanical observations during his other official duties. There is at Kew an unpublished letter of Fox's which, since, in addition to a few notes on rubber, it indicates his breadth of interests, I am publishing in its entirety at the end of this article.

The material of lacticiferous plants collected by Fox in the northwest Amazon and preserved at Kew represents an interesting survey of species and genera. Although we are concerned mainly with *Hevea* in this present article, I should point out that other genera are represented.

Castilla. *Castilla Ulei* reported as "probably *C. elastica*, though somewhat different from the type", was said to be the source of *caucho negro*, known by the Witoto name of *efacone*. It occurs in quantity only "near the Caquetá and Putumayo rivers". I met with a number of trees of *Castilla* rubber in the Igaraparaná in 1942, but I was not able to collect specimens of any.

Micrandra. According to Fox, the latex of *Micrandra minor*, known in the native tongues as *huemega* and *waketi erwicheri*, was mixed with that of *Hevea*, but continued felling of the trees was making them rare. I was able, in 1942, to collect a specimen of *Micrandra minor* along the flood-bank of the lower Igaraparaná (*Schultes 4035*). Not far distant, in a light-forested sandy savannah, I found *Micrandra siphonioides* (*Schultes 4049*) (Fig. 1). Although both species were called by the same Witoto Indian name (*wer-meger*), the natives indicated that only *Micrandra minor* had formerly been used as a source of rubber (Plates I and II). In Fox's letter published below, the tree known by the natives as *hurmega* is tentatively identified as a *Sapium*. Although *Sapium* is found in the area and can be exploited as an adulterant of *Hevea*, Fox apparently did not collect it on his trips.

Zschokkea. Fox reported that an endemic species of *Zschokkea* called *mingadotana* by the Witotos (*Fox 31*), *Z. Foxii* Stapf, likewise disappearing because of felling, gave a latex that was mixed with

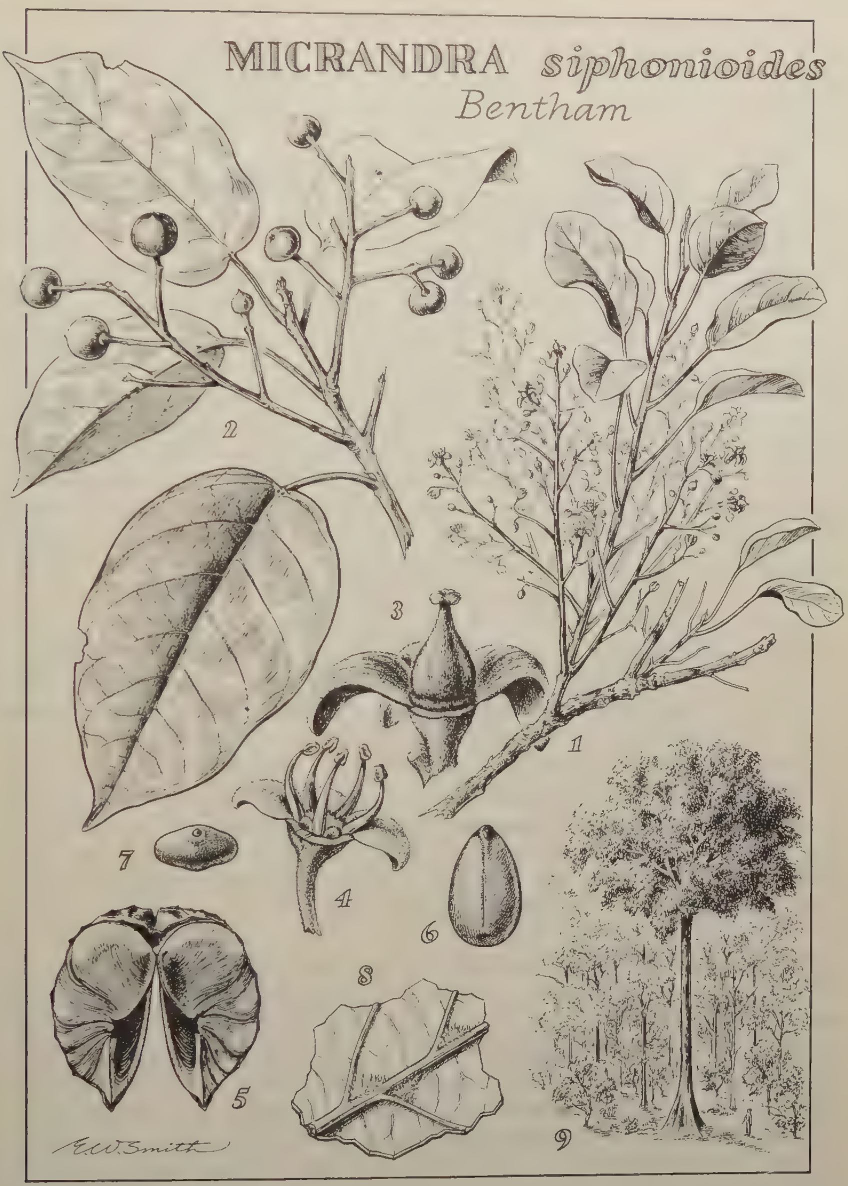


Fig. 1. *Micrandra siphonioides*

1) Flowering branch, x approximately one half natural size. 2) Branch in young fruit, x approximately one half natural size. 3) Pistillate flower, showing ovary, x approximately five times natural size. 4) Staminate flower, x approximately five times natural size. 5) Valves of capsule, x approximately natural size. 6–7) Seed, approximately natural size. 8) Portion of nether surface of leaf, showing pilosity in nerve-axils, enlarged slightly from natural size. 9) Habitat sketch of tree, showing large buttresses.

(Drawn by Elmer W. Smith)

that of *Castilla* and *Hevea*. I failed to find any *Zschokkea* producing rubber along the Igaraparaná, but a species of this genus (*Schultes 5459*) was collected in the upper Apaporis basin in the Colombian Amazonia as the source of a kind of rubber known locally as *dinde*.

Sideroxylon. The rare *arorate*, probably *Sideroxylon cyrtobotryum* Mart., was said to yield a kind of gutta on the Río Putumayo, near the Igaraparaná, but again I did not find it in production in 1942.

Couma. In the early 1940's, the lacticiferous tree most widely exploited was *Couma macrocarpa* (*Schultes 3878a*). The latex of this corpulent tree is the source of a kind of chicle employed in making chewing gum; and, during the rubber boom of the Second World War, it enjoyed a high price and was produced from wild trees in many parts of the western Amazonia. The tree is exceedingly abundant in the Karaparaná-Igaraparaná region. It is curious that it was not mentioned in Fox's notes in the Kew Bulletin article, despite the fact that it undoubtedly was not exploited in the early part of this century. The Colombian name of *Couma macrocarpa* and its product is *juansoco*; the Peruvians call it *leche caspi*; in Brazil, it is *sorva*. The Witotos of the Igaraparaná know it as *do-ko* (Plate III).

Neocouma. Another abundant apocynaceous tree of this region is *Neocouma Duckei* Mgf. (*Ambelania Markgrafiana* Monachino). The copious thick white latex of this small to medium-sized tree (*Schultes 3877*; *3877a*) is said to be the source of an inferior chicle; but, in the 1940's, it was being mixed with the latex of *Couma macrocarpa* in the production of commercial *juansoco*. *Neocouma Duckei* is called also *juansoco* or *juansoco de sabana* and *palo de leche*; the Witotos refer to it as *do-ko-gay*. I later found this species similarly used to adulterate *Couma macrocarpa* latex in the upper Apaporis basin (*Schultes 5357*) under the vernacular name *caimo morado*.

Hevea. Most of Fox's material of Hevea preserved at Kew was collected in the area that we are discussing in this paper. He did, however, provide specimens gathered on March 4, 1911, along the Río Amazonas itself, at Pebas, a Peruvian locality between Iquitos and the Colombian town of Leticia. One of these (*Fox 115*), reported as the source of *jebe fino* (the best quality of rubber), was identified by Jacques Huber as *Hevea brasiliensis*; I have examined the material at Kew and concur with this determination. The other (*Fox 116*), called *jebe débil* ("weak rubber") bears Huber's annotation as representing *Hevea nigra* Ule; it seems to me to be referable to what we now accept as *H. guianensis* Aubl.

In addition to the Kew Bulletin report to which reference has been made above, critical notes on Fox's collections of *Hevea* were published by Huber (Novas contribuições para o genero Hevea, Bol. Mus. Goeldi **7** (1913) 227–236). Fox had sent a collection of his rubber plants to Huber, then the foremost authority on the classification of

Hevea. Huber reported being able to distinguish three species in the material: "two closely related to the group of *H. lutea*, and the third a species already previously described by me but upon incomplete material".

The third of these three species was referred by Huber to *Hevea viridis*, a species which he had described in 1902 on the basis of sterile specimens from the lower Ucayali in Peru. The Fox material, since it was in flower, gave Huber opportunity to complete the description and to assign the species to series *Obtusiflorae* in his classification of the genus. *Hevea viridis* has now been placed in synonymy under *H. nitida* Martius, and there is general agreement on this disposition of Huber's binomial (SEIBERT, Ann. Mo. Bot. Gard. **34** (1947) 298; SCHULTES, Bot. Mus. Leafl. Harvard Univ. **13** (1947) 9). Noting, in topotypical cultivated material grown in the Jardim Botânico of the Museu Goeldi in Belem, a minute lepidote condition on the nether surface with scales so small and sparse that the typical concolourous character of the leaflets was not altered, Seibert suggested that Huber's type material of *Hevea viridis* had "some admixture of *H. brasiliensis* germ-plasm". My study of very ample material of *Hevea* from its entire range convinces me that small variations, especially in respect to scales and pilosity, may and should be expected without our necessarily resorting to introgression or other complex phenomena to explain their occurrence. This instance of *Hevea nitida* is a case in point: five or six of the numerous collections that I made of this species in the Colombian Vaupés, hundreds of miles from the nearest *H. brasiliensis*, show a similar minutely lepidote condition.

The two species described by Huber as "closely related to the group of *H. lutea*" are *Hevea Foxii* and *H. glabrescens.* Most of the rubber from the region between the Ríos Karaparaná and Igaraparaná was produced by the tree that Huber described as *Hevea Foxii.* "Of the rubber exported from this region, 75 per cent is derived from *Hevea Foxii*, and these trees are the only ones which are properly tapped. All the other rubber plants are cut down for the extraction of their latex." This *Hevea* was slashed with a machete. The latex was allowed to run down the trunk to the ground, coagulating as it went, and the strips were collected, washed and pressed into sausage-shaped lumps known in commerce as "Putumayo tails" or *rabos del Putumayo.*

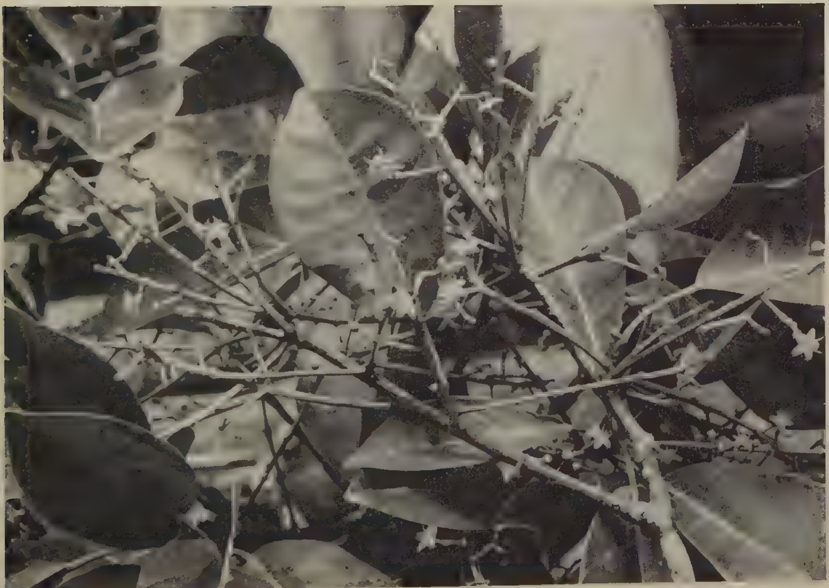
Huber distinguished *Hevea Foxii* from what was then called *H. lutea* (*H. guianensis* var. *lutea*) by its having leaflets glabrous beneath in the adult stage; while what he interpreted as "*H. lutea*" had leaflets glabrous from the start. Furthermore, he reported an indistinct disk in the staminate flower of "*Hevea lutea*" and *H. Foxii* as compared with a short, thin annular disk in *H. glabrescens.* In both of these characters, we have come now, with much wider experience, to expect appreciable variation, and neither this vagary in leaf pilosity nor the slight fluctuation in the disk can be taken as critical — unless combined with at least one more stable and more important difference. This additional difference is not found. Huber likewise stated that *Hevea Foxii* appeared to be allied to *H. apiculata* Spr. ex Baill., collected by Spruce on the Río Negro and now considered to be *H. guianensis* var. *lutea.*

Ducke and Seibert are the only recent botanists to have discussed *Hevea Foxii* and *H. glabrescens.* In 1929, Ducke (Rev. Bot. Appl. **9** (1929) 627) considered both to represent varieties and made the nomenclatural transfers *Hevea lutea* var. *Foxii* and var. *glabrescens.* In 1935, he (in Arquiv. Inst. Biol. Veg. **2** (1935) 231–232) listed *Hevea Foxii* and *H. glabrescens* as good species, pointing out, nonetheless, that they were known from sparse material. In 1946, he (in Bol. Tecn. Inst. Agron. Norte no. **10** (1946) 10, 23) suggested that both might be varieties of *H. guianensis* related to *H. guianensis* var. *lutea*; that *H. Foxii* (together with *H. apiculata* Baill., described from the upper Río Negro basin) represented possibly a geographical variety peculiar to the northwest Amazon and characterized by strong leaflet pubescence; that *H. glabrescens* might be considered a transition from *H. Foxii* to *H. guianensis* var. *lutea*; but that more material would be necessary before resolving the problem.

Seibert (loc. cit. 295), in discussing *Hevea Foxii*, stated: "It appears that this variable pubescence character has at least twice accounted for the description of separate entities, namely *H. lutea* var. *pilosula* Ducke and *H. Foxii.* Such variations, where *lutea* and *Benthamiana* grow close together, may result from further hybridization between the two entities. In other instances, these variations may be natural tendencies toward recombination. The range of variation and distribution as known from specimens at hand appear to be too intergrading for any decisive subspecific naming at the present time." Seibert referred *Hevea Foxii* to *H. guianensis* var. *lutea* x *H. Benthamiana*, because (loc. cit. 319) "leaflet pubescence, long reddish floral pubescence, and the bud and calyx lobe accumination" (shown in Fox's specimens from Liberia) are "definitely characters of *H. Benthamiana*". Unfortunately for this hypothesis, similar conditions of pubescence exist in a number of my collections of *Hevea guianensis* var. *lutea* (e.g. *Schultes 5649*, Upper Río Apaporis Basin; *Schultes & Cabrera 14329*, Río Vaupés Basin; and others) hundreds of miles from the nearest *H. Benthamiana.* In fact, the presence of reddish or golden leaflet and floral pubescence appears, in the Colombian Amazonia in general, to be the more usual condition.

Insofar as *Hevea glabrescens* is concerned, Seibert believes that Huber was confused in the several collections that he cited in the original description. *Fox 7*, the type, collected in the headwaters of the Río Igaraparaná, he determined as *Hevea guianensis* var. *lutea* x *H. Benthamiana*, thus equating it with *H. Foxii.* But Huber cited also two other Fox collections (from Sombra on the Río Putumayo and Pebas on the Amazon itself) in the original description; Seibert thought these "better placed in *H. guianensis* var. *lutea* x *H. pauciflora.*"

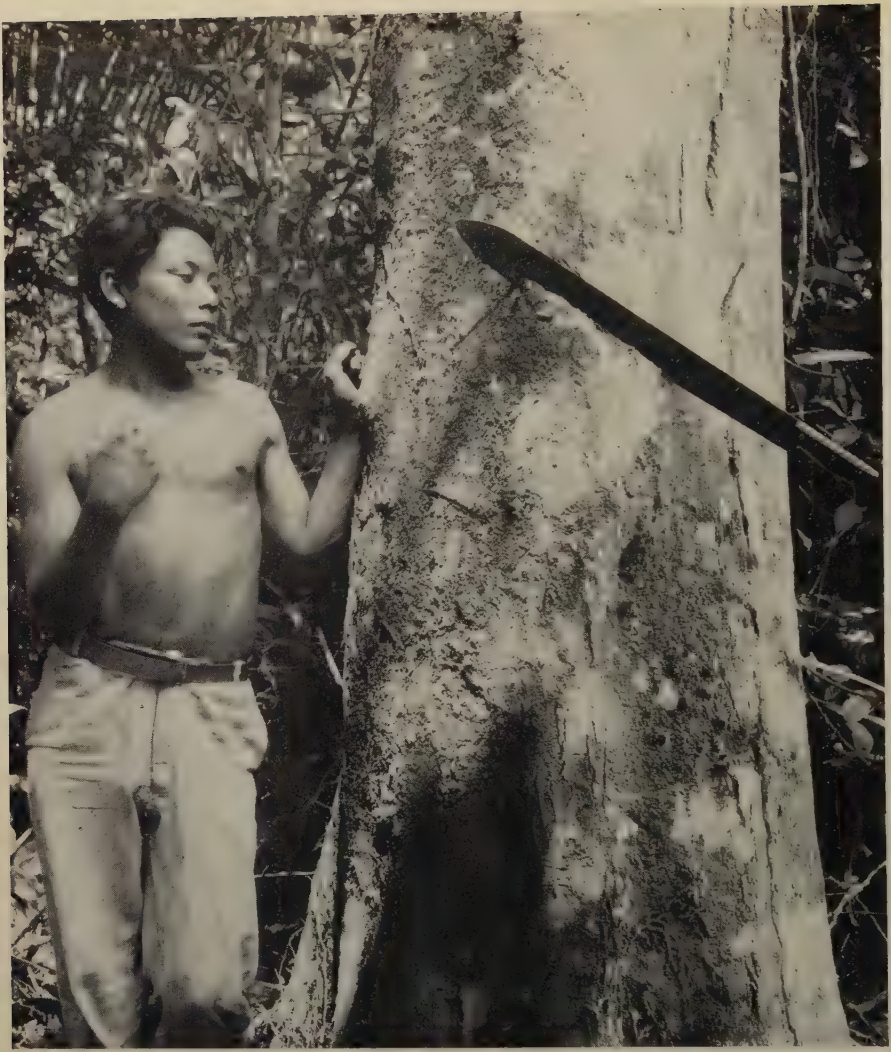
It is now clear from collections and studies of many trees of *Hevea guianensis* var. *lutea* in the northwesternmost part of the Amazon, especially in the basins of the Ríos Vaupés, Apaporis and Caquetá in Colombia, that this is the area where the variety manifests its greatest



Above: *Micrandra minor* is a conspicuous element along flood-banks of the lower Río Igaraparaná. The crown in the centre of the picture represents this species. Photographed by R. E. Schultes.

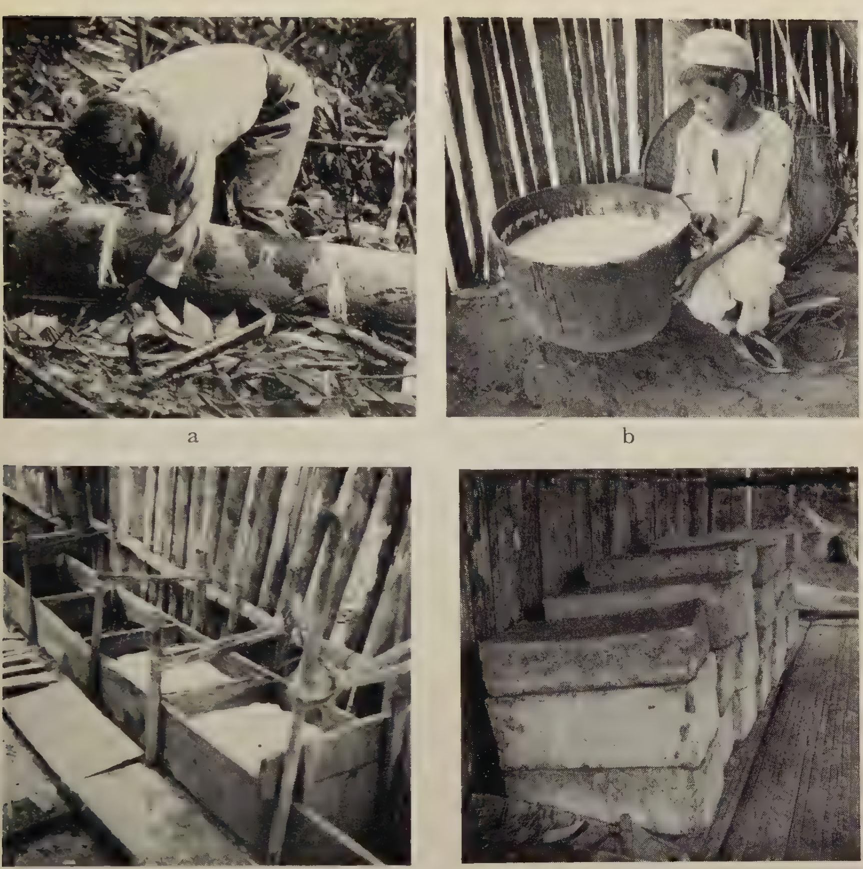
Below: Flowering branches of *Micrandra minor*.
Photographed by R. E. Schultes, Río Caquetá, Colombia.

Plate I



Unlike *Micrandra siphonioides*, with a buttressed trunk and very sparse latex, *M. minor*, pictured above, is unbuttressed and has a copious flow of thick, white milk. Photographed by R. E. Schultes. Rio Apporis, Colombia.

Plate II

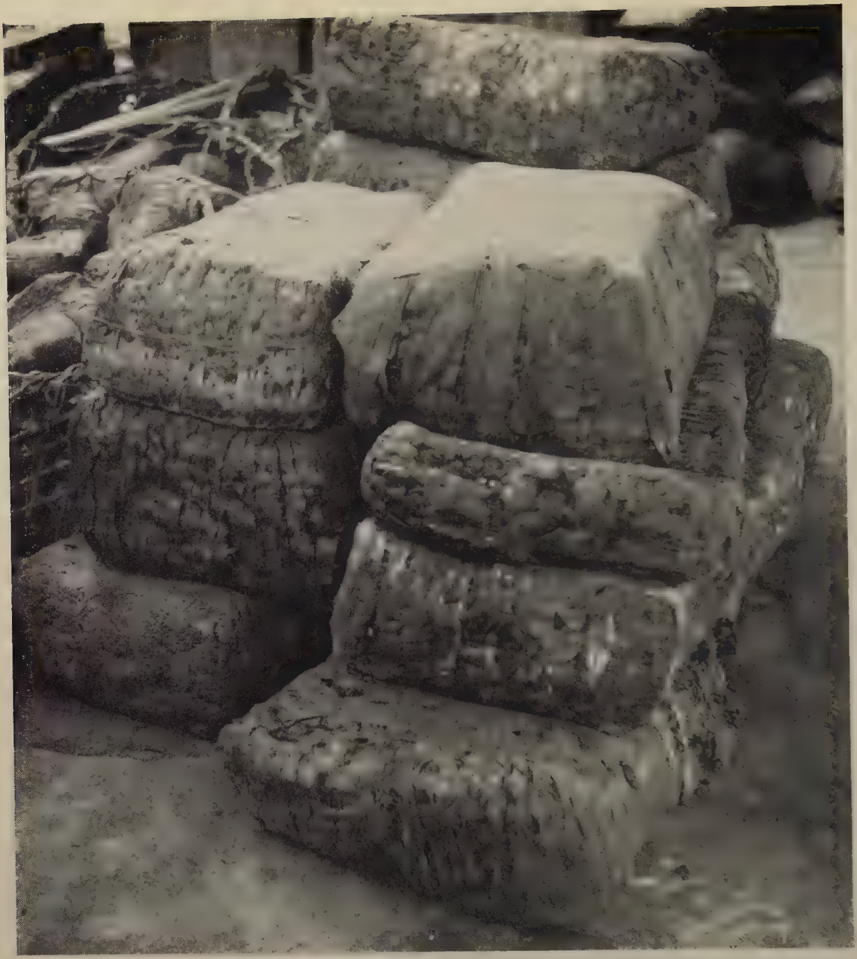


a b

c d

Couma macrocarpa is the source of *juansoco*, a kind of chicle employed commercially in making chewing gum. It is exploited actively in the Karaparaná-Igaraparaná region at the present time. The tree is usually felled and ringed and the copious latex collected in cups made of palm leaves (a); boiled in large pots; (b) poured into crude wooden moulds (c); and allowed to coagulate into large blocks (d) which are then sold for shipment to commercial centres. Photographed by R. E. Schultes. Río Karaparaná, Colombia.

Plate III



Along the Río Igaraparaná and adjacent rivers, rubber is prepared principally from *Hevea guianensis* var. *lutea* in the form of *rabos del Putumayo* ("Putumayo tails") and *Putumayo blocks.* In both cases, scrap rubber or *sernambí*, strips allowed to dry on the tree, are pressed together: in the former, in shapes simulating tails; in the latter, into large blocks, pictured above, made with crude presses. Photographed by R. E. Schultes. Río Igaraparaná, Colombia.

Plate IV

La Chorrera, principal rubber-gathering centre of the Río Igaraparaná during the first two decades of the present century. An infamous centre of mistreatment of Indian labour, it is now a mission station with schools and medical help for the Witoto Indians. Photographed by R. E. Schultes.

Plate V

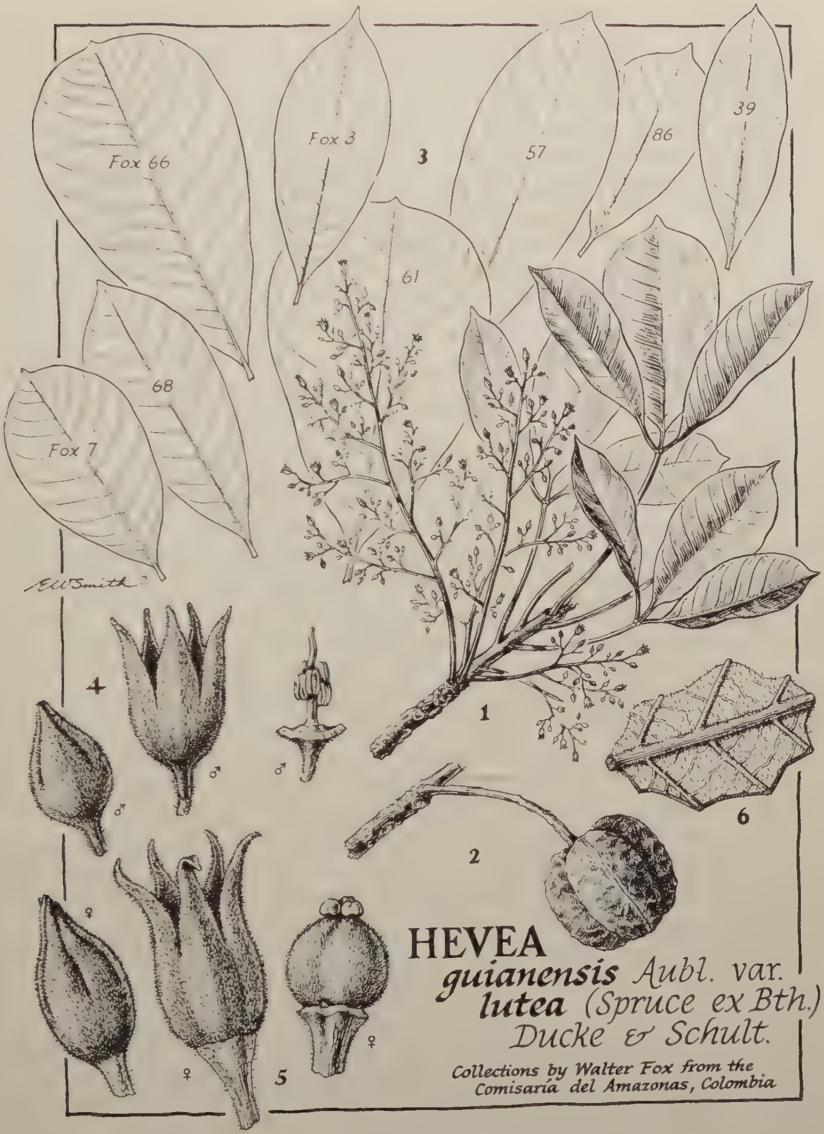

Fox 66
Fox 3
3
57
86
39
61
68
Fox 7
E.W. Smith
4
♂
♂
♂
1
6
2
♀
♀
5
♀
HEVEA
guianensis Aubl. var.
lutea (Spruce ex Bth.)
Ducke & Schult.
Collections by Walter Fox from the
Comisaría del Amazonas, Colombia

Fig. 2.

variability and that, when a sufficiently large and representative mass of material is studied, these very minor and highly variable (even on a single tree at different periods of the year) characters cannot be employed to maintain taxonomically valid concepts nor as indications of hybridization. I am, therefore, considering the material described by Huber from the Putumayo area as *Hevea Foxii* and *H. glabrescens* as simply northwestern expressions of *H. guianensis* var. *lutea* (Fig. 2).

It is curious that a collector of Fox's singular dedication to lacticiferous trees missed the presence in the lower course of the Río Igaraparaná and downstream along the Río Putumayo of *Hevea Benthamiana.* This species is not nearly so abundant in the area as *H. guianensis* var. *lutea*, and it inhabits deeply and long-flooded river banks instead of higher land that floods only lightly and for a short period each year. Since the rubber of *Hevea Benthamiana* is far superior to that of *H. guianensis* var. *lutea*, however, the natives may have tapped it during the rubber boom of the early years of this century. There is a possibility, however, that they neglected it because of its much more marshy habitat as compared with that of *Hevea guianensis* var. *lutea.* We known definitely that, in the resurgence of wild rubber work in the 1940's *Hevea Benthamiana* was worked in this area and that it was distinguished from rubber supplied by *H. guianensis* var. *lutea* (*seringa débil*) (Plate IV) by the vernacular name *seringa fina.* The collection *Schultes 4026* (Río Igaraparaná between Quebrada Menaje and the Río Putumayo, alt. 150–170 m, June 15–17, 1942. "Tree in swamps. Latex white, thick. Bark dark brown, smooth.") represents *Hevea Benthamiana* and is closely matched by *Schultes 8123, 8125, 8126,* and *8127* from the Río Putumayo near Tarapacá (Cf. SCHULTES, in Bot. Mus. Leafl. Harvard Univ. **16** (1953) 39) and other collections from the Río Caquetá near La Pedrera.

In Fox's letter published below, the source of rubber in the Igaraparaná-Karaparaná region is reported as "probably *H. Spruceana*". This was Fox's surmise in the field. No specimens of *Hevea Spruceana* have been found in his collections, and indeed this species is not known to occur in this part of the western Amazon.

Fox collections of Hevea

COLOMBIA: Comisaría del Amazonas. Río Putumayo, "Zona del Avioparaná, Sección Abisinia". *Ucu-shiringa.* Bora = *ohimeca.* "De esta goma se trabaja mucho en esta sección." *W. Fox s.n.* Det. R.E.S.: *Hevea guianensis?* (Sterile; juvenile leaves). — Río Igaraparaná, Occidente. "Tree 70′." Vernacular – iteri. October 2, 1910, *W. Fox 2.* Det. Huber: *Hevea viridis.* Det. R.E.S.: *H. nitida* (Flowering). — Río Igaraparaná, Ultimo Retiro. "Ituri. Gathered these 3 specimens about 12 miles from those gathered yesterday." October 10, 1910, *W. Fox 3.* Det. Huber: *Hevea* aff. *lutea.* Det. R.E.S.: *H. guianensis* var. lutea. — Same locality. "Tree 70′." [date not specified], *W. Fox 4.* Det. Huber: *Hevea* conf. *lutea.* Det. R.E.S.: *H. guianensis* var. *lutea* (Sterile). — Río Igaraparaná. "Tree 70'." October 9, 1910, *W. Fox 7.* Det. Huber: *Hevea Foxii* (Type). Det. R.E.S.: *H. guianensis* var. *lutea* (Flowering). — Río Igaraparaná, (?), Sur. Vernacular – *e-serie.* November 5, 1910, *W. Fox 21.* Det. Huber: *H.* cf. *lutea.* Det. R.E.S.: *H. guianensis* var. *lutea?* (Sterile). — Río Igaraparana, road to Sabana [near La Chorrera] "From largest tree seen – 9′ 3″ in circ." November 19, 1910, *W. Fox 39.* Det. Huber: *H.* conf. *lutea.* Det. R.E.S.: *H. guianensis* var. *lutea*

(Sterile). — Río Igaraparaná, Sabana. November 22, 1910, *W. Fox 57.* Det. Huber: *H.* conf. *lutea.* Det. R.E.S.: *H. guianensis* var. *lutea* (Sterile). — Río Igaraparaná, Santa Catalina.December 7, 1910, *W. Fox 61.* Det. R.E.S.: *H. guianensis* var. *lutea* (Fruiting). — Río Igaraparaná, Santa Catalina. "A tall thin tree 50′ tall. Leaves more coriaceous than H. braz. Latex cream coloured", December 3, 1910, *W. Fox 66.* Det. Huber: *H. Duckei?* Det. R.E.S.: *H. guianensis* var. *lutea* (Sterile). — Río Igaraparaná, Sombra. December 24, 1910, *W. Fox 68.* Det. Huber: *H. Foxii* var. *glabra.* Det. R.E.S.: *H. guianensis* var. *lutea* (Fruiting). —Río Igaraparaná, Liberia. "Flowers yellowish". January 17, 1911, *W. Fox 86.* Det. Huber: *H. Foxii* var. *glabra* (Type). Det. R.E.S.: *H. guianensis* var. *lutea* (Flowering). — Río Igaraparaná, La Florida. January 4, 1911, *W. Fox 98.* Det. Huber: *H. cuneta?* Det. R.E.S.: *H. guianensis* var. *lutea?* (Sterile).

PERU:Departamento del Loreto, Río Amazonas, Pebas. "Vernacular – *jebe fino.*" March 4, 1911, *W. Fox 115.* Det. Huber: *H. brasiliensis* (Sterile). – Río Amazonas, Pebas. "Vernacular – jebe débil." March 4, 1911, *W. Fox 116.* Det. R.E.S.: *H. guianensis?* (Sterile).

We may summarize the synonymy of *Hevea guianensis* var. *lutea*, as at present understood, as follows:

Hevea guianensis *Aublet* var. **lutea** (*Spr. ex Benth.*) *Ducke & Schultes* in Caldasia 3 (1945) 249.

Siphonia lutea Spruce ex Bentham in Hooker Kew Journ. 6 (1854) 370.

S. brevifolia Spruce loc. cit. 7 (1855) 194, *nomen nudum.*

S. apiculata Spruce ex Baillon in Adansonia 4 (1864) 285.

H. lutea (Spr. ex Benth.) Mueller-Argoviensis in Linnaea 34 (1865) 204.

H. lutea (Spr. ex Benth.) Mueller-Argoviensis var. *apiculata* (Spr. ex Baill.) Mueller-Argoviensis in Martius Fl. Bras. 11, pt. 2 (1874) 302.

H. peruviana Lechler ex Bentham & Hooker Gen. Pl. 3 (1880) 290.

H. lutea (Spr. ex Benth.) Mueller-Argoviensis var. *cuneata* Huber in Bol. Mus. Goeldi 3 (1902) 357.

H. cuneata (Hub.) Huber loc. cit. 4 (1906) 626.

H. brasiliensis (Willd. ex Adr. Juss.) Mueller-Argoviensis var. *cuneata* (Hub.) Pax in Engler Pflanzenr. 4 (1910) 123.

H. Foxii Huber ex Fox in Kew Bull. 1912 (1912) 74, *nomen nudum.*

H. Foxii Huber in Bol. Mus. Goeldi 7 (1913) 228.

H. glabrescens Huber loc. cit. 7 (1913) 230.

H. lutea (Spr. ex Benth.) Mueller-Argoviensis var. *Foxii* (Hub.) Ducke in Rev. Bot. Appl. 9 (1929) 627.

H. lutea (Spr. ex Benth.) Mueller-Argoviensis var. *glabrescens* (Hub.) Ducke loc. cit. 9 (1929) 627.

H. lutea (Spr. ex Benth.) Mueller-Argoviensis var. *peruviana* (Lechl. ex Benth. & Hook.). Ducke loc. cit. 9 (1929) 627.

H. guianensis Aublet var. *cuneata* (Hub.) Ducke in Arch. Jard. Bot. Rio Jan. 6 (1933) 51, *pro parte.*

H. lutea (Spr. ex Benth.) Mueller-Argoviensis var. *pilosula* Ducke loc. cit. 6 (1933) 53.

H. lutea (Spr. ex Benth.) Mueller-Argoviensis var. *typica* Ducke loc. cit. 6 (1933) 53.

H. lutea (Spr. ex Benth.) Mueller-Argoviensis fma. *pilosula* (Ducke) Ducke in Arch. Inst. Biol. Veg. Rio Jan. 2 (1935) 224.

H. guianensis Aublet var. *lutea* (Spr. ex Benth.) Ducke & Schultes fma. *peruviana* (Lechl. ex Benth. & Hook.). Ducke in Bol. Tecn. Inst. Agron. Norte, no. 10 (1946) 24.

H. guianensis Aublet. var. *lutea* (Spr. ex Benth.) Ducke & Schultes fma. *pilosula* (Ducke) Ducke loc. cit. no. 10 (1946) 24.

A word remains to be said about the vernacular and Indian names for rubber and rubber-producing trees in the Karaparaná-Igaraparaná region of Colombia's Amazonas. The following list has been drawn up from my own observations (S) and those of Fox (F).

caucho negro (S)		*Castilla elastica*
do-ko (S)	Witoto Indians	*Couma macrocarpa*
do-ko-gay (S)	Witoto	*Neocouma Duckei*
efacone (F)	Witoto	*Micrandra minor*
ee-te-ree (S)	Witoto	*Hevea guianensis* var. *lutea*
e-serie (F)	Witoto (?)	*Hevea guianensis* var. *lutea*
huermega (F)	Witoto	*Micrandra minor*
wer-me-ger (S)	Witoto	*Micrandra minor* and *M. siphonioides*
ituri (F)	Witoto	*Hevea guianensis* and *H. guianensis* var. *lutea*
juansoco (S)		*Couma macrocarpa* and *Neocouma Duckei*
juansoco de sabana (S)		*Hevea guianensis* and *H. guianensis* var. *lutea*
ohimeca (F)	Bora Indians	*Hevea guianensis*
palo de leche (S)		*Neocouma Duckei*
seringa de rebalse (S)		*Hevea Benthamiana*
seringa fina (S)		*Hevea Benthamiana*
ucu-shiringa (F)		*Hevea guianensis*
wakati erwickeri (F)	Bora (?)	*Micrandra minor*

Fox's letter, written from the rubber-gathering centre of the Peruvian Amazonas Corporation (Casa Arana) at La Chorrera on the Río Igaraparaná, is reproduced because of its botanical and historical interest. The original letter is preserved at Kew. I have inserted within brackets several botanical identifications or critical notes.

La Chorrera, Peru
13 Nov., 1910

Dear Col. Prain:

I have never thanked you for sending on board for me the collecting outfit you had so kindly promised me. It has been most useful. Indeed, if I could have done always what I should have liked, it would have been to have stayed in suitable spots and collected. Largely, as it is, I can only gather any striking thing and that must be fairly easily get-attable [sic]. Well this is an immense country, a magnificent country, and for the equator a lovely climate. In the hands of an enterprising people, what could not have been done with it? As it is, however, to say that it is backward is to state a fact that is well known to most people in Europe. I think you know that part of our enquiries is to look into the alleged atrocities said to have been and are being carried on in the Company's territory against the Indians. I wish not to anticipate our reply to that further than that I should like to exterminate 5/6 of the employees here who are placed over unfortunate aborigines. The whole system of management is wrong from top to bottom. The method of working the rubber is of the most primitive and crudest imaginable in the way of a better system simply because those placed over them know no better. One chief of section went so far as to say that he only knew a rubber tree when he saw it exuding latex. I was much surprised with the magnitude of the Amazon, the monotony was only relieved by its vastness—going along day after day, with much the same general scenery confined, of course, to the immediate shores, as the whole Amazon basin is so flat that the vision is shut in by the two shores. Perhaps the commonest trees along the bank were the Cecropias—and on the innumerable sandbanks called "playas" the arrow grass, a Saccharum I think [*Gynerium sagittatum*]. If I was asked my impressions of the American forests as compared with the Malayan jungles, I should give the palm to the latter—that is, vegetation is denser, trees bigger—but, of course, I have not yet been in the Brazilian forests except for a little bit of the forest near Pará—so that the comparison is of no value. If you look at a map of America, you will see the river Putumayo—or Iça as it is called at its mouth where it empties into the Amazon. About 3 days steaming up the

Putumayo brings one to the 2 tributaries—the Igaraparaná and the Caraparaná, and it is practically the basins of these two tributaries that the Company claims as its sphere of operations— roughly some 14 or 15 000 square miles. This territory has been divided up into sections. Over each section, a chief assisted by several so-called white men is appointed, and owing in a great measure to the pernicious system of paying the chief by results, it is his policy to get as much rubber as he can in the shortest space of time. And here is where the exploitation of the poor wretches of Indians comes in. I will tell you more of this when I see you—in the course of our enquiry we are visiting these sections—using the two rivers as far as possible, but most of our journeys are on foot through the worst jungle tracks I have yet seen. Distances here are reckoned by time instead of miles, i.e. such and such a place is so many hours or days away. I have never done so much jungle walking in the same time before. So far I have found that the rubber from this region is mainly produced by Hevea probably *H. Spruceana* [see discussion above], but of this I am not quite sure. I have collected specimens, but have no fruits so far. Then there is another tree called by natives "Hurmega", which is probably a *Sapium* [see discussion above], and thirdly another tree that I am not sure what it is, but as I am bringing home specimens I hope to clear it up. So far I have not come across a single Castilloa. Orchids so far have been almost completely absent. I collected one small plant with orchid pseudobulbs and monophyllous leaves with a pendant inflorescence—of a distinctly bluish colour [*Aganisia cyanea*], common along the Río Karaparaná. [See Schultes in Lloydia 21 (1958) 88 and in Am. Orch. Soc. Bull. 30 (1961) 558.] I have dried the flowers and hope to bring the plant alive. I have one or two other things but, on the whole, I am disappointed as regards Orchids. On the other hand, I have a few seedlings in a box of a lovely slender bamboo rivalling asparagus plumes in feathery grace —also some palm seeds of several sp. Melastomaceae is very common—so is Bignoniaceae—some of the latter are truly giant. There is also a beautiful thing in the forest here with large white bracts and small lilac flowers, probably a Mussenda. I have specimens but alas no seeds. Before I get back I hope to have quite a nice little collection of seeds. As far as I can see, we ought to drive home about May. This is, however, so subject to circumstance that it is only an indication I want to be back a little before the Rubber Exhibition.

With kindest regards,
Yours sincerely,
Walter Fox

Acta Botanica Neerlandica **15** (1966) 190–192

NOVITATES FLORAE AEGYPTIACAE I

M. ABDALLAH(1) AND F. SA'AD(2)

*(Herbarium Section (CAIM), Ministry of Agriculture
DOQQI, U.A.R. (Egypt))*

(received November 18th, 1965)

Convolvulus austro-aegyptiacus Abdallah & Sa'ad, nov. spec. (Subser. *Diffusi* Boissier, Fl. Or. **4**: 85. 1875).

Planta perennis, herbacea, procumbens, hirsuto-puberula; a basi ramosa, caudice lignoso; caules 30–90 (–120) cm longi, simplices vel dimidio inferiore ramosi; folia herbacea, hirsuta, radicalia anguste obovata, acuta, basi sensim attenuata, 3–5 cm longa, 3–6 mm lata, 8–10 × longiora quam lata, caulina oblonga vel anguste obovata, acuta vel subacuta, basi attenuata, 1.5–4 cm longa, 3–10 mm lata, 4–8 × longiora quam lata; flores axillares, usque ad 7 inflorescentiam dichasiali-monochasialem vel monochasialem efformantes raro abortu solitaria, pedunculo bractea multo longiore; bracteoli oblongi vel lineares; sepala hirsuta, exteriora 7–8 mm longa, oblonga vel anguste obovata, longe acuminata, medium marginibus inaequalibus, interiora 6–7 mm longa, late oblonga, longe acuminata, basi truncata; corolla 1.3–1.5 cm longa, calyce bis longiore, limbo pallide roseo, tubo albo; stamina inaequalia, filamentis glabris; pistillum glabrum, stylo filiformi, stigmatibus filiformibus, stylo 1.5 × longioribus; capsula non visa. **Fl. Mart. – Apr. Fr. . .**

Typus: Abdallah s.n., U.A.R. (Egypt), El-Allâqi (Nile Valley), 21.3.1962, holotypus (U), isotypus (CAI, CAIM, K, WAG).

Additional characters: stems cylindrical, flowering in the upper half; leaves green with conspicuous costa, bracts like the leaves; bracteoles not exceeding the calyx, but if the number of the flowers in the inflorescence is more than three the bracteoles of the older flowers enlarged, exceeding the calyx; sepals slightly unequal, the upper part green, the lower colourless, the middle one with one side membranous, the colourless part of the inner ones convex, with the two sides glabrous, membranous; corolla turning white when withering, without distinct lobes, with hairy bands outside but the lower part of the limb and the tube quite glabrous; the longest stamen 7 mm, anthers oblong slightly

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[1] Laboratorium voor Plantensystematiek en -geografie, Wageningen, Netherlands.

[2] Instituut voor Systematische Plantkunde van de Rijksuniversiteit, Botanisch Museum en Herbarium, Utrecht, Netherlands.

notched above; ovary ovoid, with a glabrous fleshy cup-shaped disc at the base. (Fig. 1).

Vernacular name: Agwādeīt (Baššārī).
Distribution: Southern U.A.R. (Egypt). (Fig. 2).
On sandy cultivated ground, canal banks.

Specimens seen:
U.A.R.: Abdallah s.n., Dakhla Oasis (Western Desert), Budkhulu, 23.4.1961 (CAIM). Abdallah & Mahdy 1667, El-Allâqi (Nile Valley), (CAIM); ibid., Sa'ad & Abbas 1670 (CAIM).

Our species differs from *C. pilosellaefolius* Desr. by its narrowly obovate or oblong cauline leaves, bracts like the leaves, oblong or narrowly obovate, long-acuminate sepals; from *C. microphyllus* Sieb. ex Spreng. by its larger leaves, lax inflorescence on a very long peduncles much longer than the subtending bract.

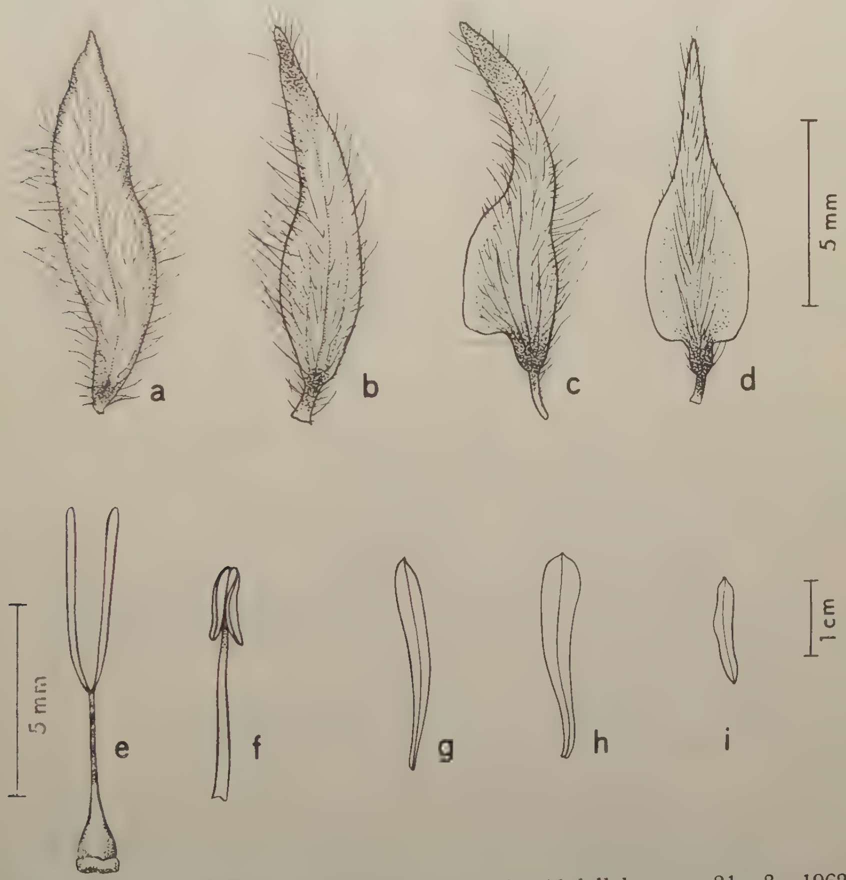

Fig. 1. *C. austro-aegyftiacus* Abdallah & Sa'ad: Abdallah s.n., 21. 3. 1962, holotype (U).
(a) bracteole; (b) outer sepal; (c) middle sepal; (d) inner sepal; (e) pistil; (f) stamen; (g) radical leaf; (h) cauline leaf; (i) bract.

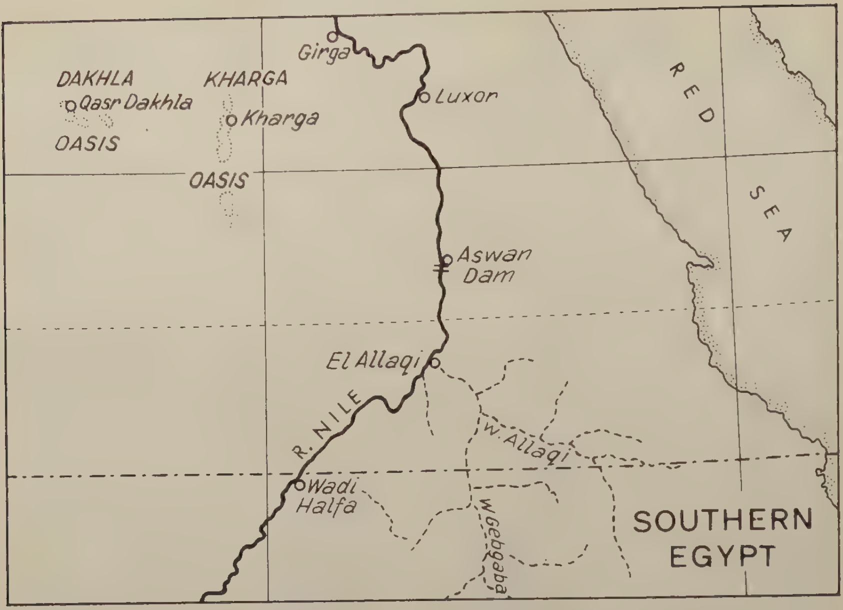

Fig. 2. Distribution of *C. austro-aegyptiacus* Abdallah & Sa'ad.

The authors wish to express their gratitude to Dr. K. U. Kramer, who kindly contributed the latin diagnosis and revised the English text, and to Miss. E. M. Hupkens van der Elst and Mr. T. Schipper for the drawings.

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SOME NEW PARONYCHIAS FROM TURKEY

MOHAMMAD NAZEER CHAUDHRI
(*Botanical Museum and Herbarium, Utrecht*)

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This paper forms a part of the general study of the Subtribe *Paronychiinae* undertaken by the author for his doctoral dissertation. The publication of the new taxa, in a separate form, has been necessitated by the fact that the Flora of Turkey, covering the Family *Caryophyllaceae*, is to be published in the near future, at any rate before the author can present a consolidated account of the results of his own study of the group.

The present paper deals only with the diagnosis and description of the new taxa, presented in a rather conventional manner, and no attempt is made to go into details of the various morphological and taxonomic problems pertaining to the genus *Paronychia* as a whole. Such problems will, of course, be taken up in the general revision of the group.

Almost all the new taxa described here, though very distinct and well-marked, are known from one or two gatherings only, mostly from one locality, and thus seem to be endemic. It must, however, be pointed out, in this connection, that so far as the genus Paronychia is concerned, Turkey is, undoubtedly, the richest region in the whole world; and notwithstanding the extensive collections made by Sintenis, Bornmüller, Davis and others, there still remain large areas of the country virtually untouched and unbotanized. Moreover, some of the previously described and better known species, such as *Paronychia cephalotes* (M. B.) Bess., *P. arabica* (L.) DC., and *P. polygonifolia* (Vill.) DC., which are quite widespread in the adjoining areas, have been recorded during the nineteenth century (there being no record for these species during the past sixty-five years) from one or two places only. The apparent endemism of the new taxa might, therefore, be ascribed to the scantiness of the material rather than to any other factor.

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spite of a heavy pressure of official work, helped in typing out the manuscript.

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Material from the following herbaria was examined: Budapest University (BPU); Copenhagen (C); Edinburgh (E); Geneva (G); Halle (HAL); Hamburg (HBG); Jerusalem (HUJ); Jena (JE); Leiden (L); Lund (LD); Stockholm (S); Stuttgart (STU); Tbilisi (TGM); Utrecht (U); Vienna (W); Vienna University (WU); Zürich (Z).

All species described here are small perennial herbs and belong to *Paronychia* sect. *Anoplonychia* Fenzl.

1. **Paronychia galatica** Chaudhri sp. nov. (Plate IV, Fig. 10)

Planta prostrata vel breviter decumbens. Caulis ramosissimus. Rami validi, internodiis 5–9 mm longis, dense breviterque pilosiusculi. Folia anguste elliptica vel lanceolata 3–6 × 1.5–2 mm, apice acuta, facie appresse hirta, pilis marginalibus rigidioribus. Stipulae lanceolatae 3–4 × 1–1.5 mm, foliis plerumque breviores, deinde valde dissectae, binae in nodo. Capitula 6–8 mm lata, terminalia lateraliaque. Bracteae oblique oblatae, acutae, 5 × 3–4 mm, flores superantes. Flores anguste ellipsoidei, omnino dense et appresse pilosiusculi, sepala subaequalia, atrovirescentia, lanceolata vel anguste ovata, apice acuto, pilosissimo. Petala 0.6–0.75 mm longa, filiformia, staminibus paulo breviora. Antherae validae, oblongae, 0.4–0.5 × 0.25 mm., pallide brunneae, filamentis subaequales. Ovarium ovoideum, 1 × 0.6 mm. Styli bini, erecti, 0.75 mm longi.

Type: Turkey, Cankiri, alt. 800 m. P. H. Davis 21508 (U, holotype; E, isotype), collected 5–6–1954.

Distribution and Ecology: Endemic in Northern Turkey. Growing on very eroded gypsaceous hills, alt. 800 m.

2. **Paronychia dudleyi** Chaudhri sp. nov. (Plate III, Fig. 8).

Planta compacta, caespitosa, caulis ramosissimus, lignosus, nodosus. Rami intertexti, capitulis crebris operti. Internodia 2–5 mm longa, imprimo pubescentes, deinde glabrescentes. Folia anguste oblonga vel oblanceolata, 3–5 × 1–1.75 mm, apice obtusa vel subobtusa, puberula, folia novella recurvata, stipulae 3–4 × 1–1.5 mm, lanceolatae, plerumque foliis paulo breviores vel subaequales, sed ad apices ramulorum longiores. Capitula globosa 6–10 mm lata, creberrima, plantam fere obtegentia, confluentia. Bracteae oblique ovatae, 4–5 × 3–4 mm, flores superantes sed non obtegentes. Flores ellipsoidei, 2.5–3.25 mm longi, dense et adpresse pubescentes. Sepala subinaequalia, lanceolata vel anguste oblonga, acuta, interiora scaphoidea. Petala stamina superantia, 0.8–0.9 mm longa. Ovarium ovoideum, styli bini erecti, 0.6–0.7 mm longi. Fructus calyce obtectus, pericarpium annulo collari manifesto.

Type: Turkey, Prov. Eskişehir, Ankara to Sivrihisar, 20–30 miles from Polatli, alt. 1000 m. Dudley, D. 36024 (U, Holotype; E, Isotype), collected on 21–6–9162.

Distribution and Ecology: Endemic, known only from the type locality, but reported to be common there.

Limestone, Artemisia steppe, alt. 1000 m.

3. **Paronychia angorensis** Chaudhri sp. nov. (Plate V, Fig. 12).

Planta compacta, caespitosa, radice crassa, longa, simplici. Caules basi ramosissimi, sat breves. Internodia inferiora brevia, superiora longiora, pubescentia vel glabrescentia. Folia anguste oblonga-oblanceolata, 2–3.5 × 0.5–1 mm, appresse pubescentia, nitidissima, valde decurvata. Stipulae lanceolatae, foliis fere aequales, deinde valde fissae. Capitula 5–10 mm lata, globosa, terminalia, confluentia. Bracteae oblique oblongae, 4 × 3 mm, flores superantes. Flores anguste oblongi-ellipsoidei, 2–2.5 mm longi, dense et appresse pubescentes, nitidissimi. Sepala fere omnia aequalia, anguste oblonga, sat carnosa, apice subobtuso, ciliifero. Petala 1–1.25 mm longa, staminibus longiora. Ovarium ovoideum, stylis binis, erectis. Fructus calycem omnem replens.

Type: Turkey, Vilayet Ankara, Beynam. P. H. Davis 13103 (U, holotype; E, isotype), collected 5–7–1947.

Distribution and Ecology: Endemic in the northwestern region of Turkey, west of Ankara. "Steep shaley slope facing south in woods".
Paratype: Turkey, Vilayet Ankara, Beynam. De Koster, de Wall Repelaer, Croockewit and Maas Geesteranus, s.n. (U), collected 23–6–1951.

4. **Paronychia cataonica** Chaudhri sp. nov. (Plate III, Fig. 7).

Planta caespitosa, compacta, prostrata. Caulis ramosissimus, basi lignosus. Rami longi, validi. Internodia 4–8 mm longa, valida, puberula vel deinde subglabrescentia. Folia elliptica, 3–4 × 1.5–2 mm, adpresse pubescentia, crassiuscula. Stipulae lanceolatae, 4–5 × 1.25–1.5 mm, folia superantes, binae in nodis sed deinde fissae. Capitula creberrima, coalescentia, 7–10 mm lata. Bracteae oblique ovatae, 5–6 × 3–4 mm, flores superantes. Flores ellipsoidei, 3–3.25 mm longi, omnino adpresse pilosi, sepala crassa, plurima aequalia, suboblonga vel anguste elliptica, apice obtusa et ciliata. Petala filiformia 0.9 mm longa; filamentis iis paulo longiora, 1 mm longa; antherae oblongae, aurantiacae, 0.4 × 0.25 mm, ovarium ovoideum, styli bini, erecti. Calyx fructu dimidio longior.

Type: Turkey, Prov. Malatya, Malatya-Maras, 70 km from Malatya, alt. 1450 m, collected 9–6–1960. Stainton and Henderson 5489 (U, holotype; E, isotype)

Distribution and Ecology: Endemic in the type locality, around Malatya. "Growing on wasteground along roadside," alt. 1400 m.
Paratype: Prov. Malatya, Gurun-Darende, alt. 3500 ft., calc. steppe. P. H. Davis 21937 (E), collected on 19–6–1954.

5. **Paronychia turcica** Chaudri sp. nov. (Plate IV, Fig. 9).

Planta compacta, caespitosa, suffrutescens; caulibus basi lignosis, ramosissimis, nudis, induratis, valde intricatis. Rami validi. Internodia brevia, 1–2 mm longa, glabrescentia, subtus foliis et stipulis obtecta. Folia elliptica vel anguste obovata, 3–3.5 × 1.5–2 mm, crassiusculo-carnosa, valde approximato-imbricata, puberula, obtusa, stipulae lanceolatae, 5–6 × 1.5–2 mm, folia multo superantes. Capitula ovoidea vel globosa, 13–17 mm lata, terminalia, copiosa et crebra. Bracteae oblique et late ovatae, acutae, 7–8 × 3–4 mm, flores multo superantes. Flores ellipsoideo-oblongi, 2.75–3 × 1.5–2 mm, adpresse pubescentes vel puberuli, sepala inter se aequalia, oblonga, obtusa, sat lata (1 mm), perspicue trinervia. Petala 0.75 mm longa. staminibus subaequalia. Filamenta 0.6–0.7 mm longa. Antherae validae, 0.4–0.5 × 0.25 mm, oblongae, aurantiaco-brunneae, ovarium ovoideum, 0.5–0.6 mm, styli bini, erecti, 1 mm longi. Fructus ovoideus vel globosus, calyce dimidio brevior.

Type: Turkey, Prov. Bitlis/Van; Mt. S. E. of Pelli by 10 km, alt. 9000 ft. P. H. Davis 22565 and O. Polunin (E), collected 8–7–1954.

Distribution and Ecology: Endemic in the eastern region of Turkey. Growing at quite high altitudes. 9000 ft.

6. **Paronychia paphlagonica** Chaudhri sp. nov. (Plate III, (Fig.6)

Planta prostrata, basi suffrutescens; caulibus basi ramosissimis; ramis divaricatis. Internodia puberula vel glabriuscula, 5–10 mm longa. Folia elliptico-oblonga, 5–7 × 2–2.5 mm, post anthesin crassiuscula vel rigida, glabrescentia vel glabra, margine hirta, apice plerumque plus minus obtusa (sed ad apices ramulorum acuta), costa prominente. Stipulae lanceolatae, 3–4 × 1.5–2 mm, foliis subaequales. Capitula 8–12 mm lata, terminalia et lateralia, copiosa, crebra. Bracteae latissime et oblique ovatae vel oblique suborbiculares, 6–7 × 4–5 mm, floribus duplo majores. Flores 3 mm longi, ellipsoideo-oblongi (basi attenuata). Sepala glabrescentia vel glabra, margine apiceque hirta, inter se aequalia, elliptico-oblonga, obtusiuscula, margine scarioso et nervis conspicuis. Petala 1–1.2 mm longa, stamina paulo superantes. Antherae validae, styli bini, erecti. Fructus calycem replens, sed sepalis supra conniventibus.

Type: Turkey (Northern), Kastamonu, alt. 1100 m. P. H. Davis 21774a (E), collected 9–6–1954.

Distribution and Ecology: Endemic, confined to the type locality. Growing on hills, alt. 1100 m.

7. **Paronychia lycica** Chaudhri sp. nov. (Plate I, Fig. 3).

Planta satis parva sed compacta. Radix longa, subsimplex. Radices accessoriae numerosi. Folia elliptica vel obovata, 3–4 × 1.5–2 mm, utrinque dense hirta, apice acuta vel obtusiuscula. Stipulae laceolatae, plerumque folia subaequantes. Capitula 8–13 mm lata, ovoideo-rotundata, compacta et crebra. Bracteae suborbiculares, floribus multo majores. Flores ellipsoideo-oblongi, 2–2.5 mm longi, calyx adpresse pubescens, crassiusculo-subcarnosus. Sepala inter se aequalia, oblonga, obtusa, apice prominente ciliata, margine scarioso distincto. Petala filiformia, 1 mm longa. Antherae validae, ellipsoidae. Styli bini, erecti. Fructus calycem replens.

Type: Turkey, Prov. Antalya, distr. Lycia, Colbali Dagh, near Cukur Ardic Yayla, alt. 1700 m. P. H. Davis 15389 (E), collected 15–7–1949.

Distribution and Ecology: Endemic, known only from the type locality. Growing at rather high altitude, 1700 m.

8. **Paronychia sintenisii** Chaudhri sp. nov. (Plate V, Fig. 13).

Planta prostrata, compacta, basi lignosa, incrassata, nuda, valde ramosissima. Rami compacti, breves, dense foliosi, nodosi. Internodia brevissimo. Folia anguste obovata vel spathulata, basi attenuata, valde approximato-imbricata; valde adpresse pubescentia, pilis nitentibus. Stipulae anguste oblongae, 3–4 × 1–1.75 mm, folia inferiora aequantes, folia superiora paulo superantes, valde conspicuae, capitula parva sed copiosa et crebra, 5–7 mm lata, ovoidea, terminalia; Bracteae suborbiculares, 4 × 4 mm, floribus duplo longiores. Flores ellipsoideo-oblongi, 2–2.5 × 1–1.5 mm, adpresse pubescentes vel pilosi, pilis nitentibus. Sepala inter se aequalia, oblonga, obtusa et apicem verus pilis erectis, margine membranaceo

prominente. Petala 1 mm longa, filiformia, stamina paulo superantia. Antherae minutae. Ovarium ovoideum, styli bini, erecti. Fructus ampulliformis, calycem replens, stylis exsertis.

Affinis *Paronychiae chionaeae* Boiss. a qua habitu, forma foliorum, stipularum, bractearum, florum et fructuum differt.

Type: Turkey, Mt. Ida (Kaz Daghi), N 39° 43′, E 26° 48′. P. Sintenis 418/418a (LD, holotype; G, W, E, isotypes), collected 1–8–1883.

Distribution and Ecology: The species seems to be distributed over the northern part of Greece and extends to the north-western coastal strip of Turkey, around Kaz Daghi. Growing in rocky places.

Paratype: Greece, Macedonia occidentalis, distr. Kosani, in monte Vourinon, in declivibus orientalibus, subst. serpent. in saxosis, alt. 1800 m. K. H. Rechinger 17493 (W), collected 7–7–1956.

9. **Paronychia davisii** Chaudhri sp. nov. (Plate I, Fig. 2)

Planta divaricato-prostrata, basi lignosa et ramosissima. Radices accessoriae nullae. Rami longi. Internodia pubescentia-puberula vel glabriuscula. Folia elliptica vel anguste oblonga, 3–4 × 1–2 mm, dense pilosa, pilis nitidissimis, obscure carinata. Stipulae anguste lanceolatae, folia plerumque subaequantes (vel paene aequantes ad apices ramulorum). Capitula compacta, terminalia, globosa, 12–22 mm lata, distincta. Bracteae late elliptico-rotundatae, 4–6 × 3–4 mm flores occultantes. Flores 2.75–3.25 mm longi, anguste oblongi, dense et adpresse pilosi, pilis nitidissimis, sepala inter se aequalia (sed post anthesin paene subaequalia), anguste oblonga, apice obtusiuscula et ciliata, margine membranaceo prominente. Petala 0.8–0.9 mm longa. Stamina brevissima. Ovarium ovoideum, styli bini, erecti, apicibus stigmatosis aliquantum divergentibus. Fructus ampulliformis, calycem replens; sepala conniventia.

Type: Turkey, Vilayet Antalya, Takhtali Dagh (Kemer), alt. 2200 m. P. H. Davis 14121 (E), collected 16–8–1947.

Distribution and Ecology: Endemic, known only from the type locality. Growing on rocky slopes and screes, alt. 2200 m.

10. **Paronychia mughlaei** Chaudhri sp. nov. (Plate VI, Fig. 14).

Planta compacta, prostrata, laxe caespitosa. Caulis basi ramosissimus.Internodia herbacea, 5–10 mm longa, dense pilosa. Folia anguste obovata 4–6 × 1.5–2.5 mm, omnino dense et appresse pilosa, sat crassiuscula. Stipulae lanceolatae-suboblongae, 3–5 × 1.5–2 mm, plerumque foliis breviores sed ad apices ramulorum iis subaequales vel paulo longiores, binae in nodo, deinde aliquantum fissae. Capitula 10–12 mm lata, globosa, terminalia, crebra sed distincta. Bracteae late ovatae 5–7 × 3–5 mm, flores omnes operientes. Flores ellipsoidei, 3–3.25 mm longi, dense villosi. Sepala anguste oblonga, apice obtuso-pilosa,inter se paulo inaequalia. Petala filiformia, 1 mm longa. Stamina brevia. Ovarium ovoideum, stylis binis, erectis, longis. Sepala conniventia.

Type: Turkey, Prov. Mughla, Mughla to Kale, 16 km, from Mughla, alt. 1250 m, Dudley D. 35084 (E, holotype). collected 28–5–1962.

Distribution and Ecology: Endemic in the south-western region of Turkey. Growing on limestone cliffs and screes. alt. 1250 to 2100 m.

Paratypes:

1) Prov. Denizli (Caria), Boz Dagh alt. 1829–2132 m Screes. P. H. Davis 13393 (E,U), collected 16–7–1947.

2) Cilician Taurus, Burujik, Kuçuk Kur, "Limestone rocks and screes", alt. 5500 ft. E. K. Balls 1345 (E,K), collected 9–6–1934.

11. **Paronychia kotschyana** Chaudhri sp. nov. (Plate I, Fig. 1).

Planta prostrata, laxe caespitosa, suffruticosa, caules basi lignosi, indurati, ramosissimi. Rami validi, divaricati, nodosi. Internodia brevissima, puberula vel glabrescentia, plerumque foliis et stipulis obtecta. Folia elliptica vel anguste obovata, 4–6 × 1.5–2.5 mm, basi attenuata, apice acuta, dense et adpresse pilosa, pilis albis, longis, nitidis mollisque, (folia) valde approximata-imbricata. Stipulae 4–5 × 2 mm, suboblongae, foliis inferioribus subaequales, superiores ad apices ramulorum paulo superantes. Capitula ovoidea, 15–16 mm lata, terminalia et distincta. Bracteae ovatae, 7–8 × 6–7 mm, floribus multo majores. Flores oblongi, 3.5 × 2 mm, valde et adpresse pubescentes. Sepala inter se aequalia, anguste ovata vel lanceolata, acuta, perspicue trinervia, margine scarioso prominente. Petala filiformia 1.25 mm longa, stamina superantia. Ovarium ovoideum, 1 × 0.6 mm. Styli bini, erecti. Fructus maturus ampulliformis, sursum attenuatus, stylis exsertis.

Differt a *Paronychia chionaea* Boiss. habitu, forma et structura foliorum, stipularum, bractearum, sepalorum, et fructuum.

Type: Turkey ("Syria borealis"), Mt. Amanus, prope Beilan Theodor Kotschy 66 (S, holotype; JE, L, C, isotypes) collected 23–6–1862, alt. 2000 ft.

Distribution and Ecology: Endemic in the Amanus and Cassius mountain ranges, in the southern strip of Turkey just west or northwest of Syria. Inhabiting calcareous rocks, alt. 2000–5500 ft.

Paratypes:

1) Ed. Boissier, S. N. (G), Mt. Cassius, collected 5–7–1846
2) Manoog Haradjian 3136 (G, W, S, E,), Mt. Cassius, 4–5500, collected 6–1909.
3) Labillardiere S. N. (G), "Syria", collected-1787.

12. **Paronychia amani** Chaudhri sp. nov. (Plate II, Fig. 5).

Planta compacta, prostrata, basi lignosa, suffruticosa, caulibus ramosissimis, nodosis, ramis intricatis. Folia satis parva, crassiuscula, elliptica, basi attenuata 2.5–3 × 1.5 mm, adpresse pubescentia, valde approximata, recurvata. Stipulae lanceolatae, 4–5 × 1–1.5 mm, folia multo superantes, conspicuae. Capitula 8–12 mm lata, copiosa, crebra. Bracteae 7 × 5–6 mm, late ovatae vel suborbiculares, floribus multo majores. Flores ellipsoideo-oblongi, 3–3.25 mm longi, sepala crassiuscula, puberula, nitidissima, inter se aequalia, elliptico-oblonga, apice acuta (vel subacuta). Petala filiformia, 1 – 1.1 mm longa. Filamenta 1.25 mm longa, antherae validae, 0.4–0.5 × 0.25 mm, oblongae, aurantico-flavae. Ovarium ovoideum vel coniforme, 1 × 0.5 mm. Styli bini, 0.8 mm longi, erecti. Fructus ellipsoideus, 2.5–2.75 × 1.5 mm, calycem fere replens.

Affinis *Paronychiae chionaeae* Boiss. a qua differt structura foliorum, stipularum, bractearum et sepalorum.

Type: Turkey, ("Syria borealis"), Montis Amanus, region d' Hasan veyli, 4–5500′ Manoog Haradjian 2276 (G, holotype; W, isotype), collected 7–1908.

Distribution and Ecology: It seems to extend from the Amanus mountains to the central region (Prov. Kayseri) of Turkey. Inhabits rather high altitudes, 4–5500′.

Paratype: Turkey, Kayseri. Heillbronn and M. Bas Osman s. n. (G), collected 7–1941.

13. **Paronychia carica** Chaudhri sp. nov. (Plate VI, Fig. 15).

Planta compacta et caespitosa, prostrata, basi ramosissima, ramis validis, intricatis. Internodia brevia, puberula vel glabriuscula. Folia anguste elliptico-oblanceolata vel anguste obovata, 3–6 × 1–2 mm, dense et adpresse pubescentia, acuta vel obtusa. Folia vetustiora crassiuscula. Stipulae lanceolatae, 3–4.5 × 0.75–1.25 mm, folia inferiora subaequantes, folia superiora ad apices ramulorum superantes. Capitula 10–12 mm lata, ovoidea, terminalia, copiosa et crebra. Bracteae oblique ovatae, 6 × 5 mm, flores occultantes. Flores oblongi vel anguste ellipsoidei, dense et adpresse pilosi, pilis mollis, nitidis. Sepala distincte inaequalia, 2 exteriora anguste oblonga, acuta, erecta, et manifesta longiora, tertium intermedium, et 2 (rarius 3) interiora breviora, oblongo-obtusa, concava, margine scarioso inflexo, apice ciliata. Petala 1 mm longa, stamina paulo superantia. Antherae validae, oblongae, pallide brunneae, styli bini, erecti, 1 mm longi, sepala apicibus conniventibus.

Statura *P. chionaeae* Boiss., a qua differt structura calycis, sepalis distincte inaequalibus.

Type: Turkey, Buba Dagh, S. of Denizli, Erik Wall s. n. (S, holotype; LD, isotype), collected 30–5–1935.

Distribution and Ecology: Endemic in the westernmost part of Turkey. Inhabiting calcareous rocky places, alt. 800 m.

14. **Paronychia condensata** Chaudhri sp. nov. (Plate IV, Fig. 11).

Planta compacta, dense caespitosa, condensato-pulvinata, prostrata. Radix lignosa, ramosissima, caules basi lignosi, ramosissimi, intertexti. Internodia 2–6 mm longa, pubescentia vel puberula, subtus foliis et stipulis obtecta. Folia oblonga vel anguste elliptica, vel spathulata, 2–3 × 0.75–1.25 mm, basi attenuata, adpresse hirta vel pubescentia, apice subobtusa. Stipulae lanceolatae 3–4 × 1–1.25 mm, folia superantes, prominentes. Capitula pauciflora 5–7 mm lata, ovoidea, copiosa et crebra, terminalia et lateralia. Bracteae late ovatae vel oblique oblongae 5.5 × 4 mm, floribus duplo majores. Flores 2–2.5 mm longi, ellipsoidei-oblongi, adpresse hirtae vel pubescentes. Sepala inter se aequalia, elliptico-oblonga, apice subobtusa. Petala filiformia, 0.75–0.8 mm longa. Filamenta 0.6 mm longa, antherae 0.4 × 0.2 mm, oblongae, aurantico-flavae. Ovarium ovoideum, 0.5 mm, styli bini, erecti, 0.6–0.7 mm longi. Fructus calycem replens.

Type: Turkey, Nigde; W. Siehe 83 (JE, holotype; G, WU, isotypes), collected 6–7–6–1897.

Distribution and Ecology: Endemic, known only from the type locality. Growing at an altitude of 1100 m.

15. **Paronychia kemaliya** Chaudhri sp. nov. (Plate II, Fig. 4).

Planta prostrata, divaricata, suffrutescens. Radices accessoriae copiosae et prominentes. Caules basi lignosi, ramosissimi. Rami longi, patentes. Folia elliptica vel obovata, basi attenuata, 3–5 × 1.5–2 mm, adpresse pubescentia, apice acuta vel subobtusa, nervis conspicuis. Stipulae anguste lanceolatae, 4–6.5 × 1–1.5 mm, folia superantes, valde fissae. Capitula 12–15 mm, lata, ovoideo-globosa, terminalia, copiosa. Bracteae oblique et late ovatae 6–7.5 mm, acutiusculae. Flores 3–3.5 mm longi, ellipsoidei, basi angusti. Sepala inter se aequalia, adpresse pubescentia, margine hirta, oblonga, apice acuta vel acutiuscula, conspicue trinervia, margine scarioso angusto. Petala filiformia, 0.8 mm longa. Filamenta 0.75

mm longa, antherae 0.5 × 0.25–0.3 mm, validae, oblongae, pallide brunneae ovarium ovoideum vel coniforme 0.75 × 0.5 mm. Styli bini, erecti.

Differt a *Paronychia chionaca* Boiss. caulibus laxe divaricatis, et structura foliorum, stipularum, calycis.

Type: Turkey, Kemaliye ("Egin", Jokardidagh). Paul Sintenis 2495 (LD, holotype; JE, G, Z, isotypes), collected 6–6–1890

Distribution and Ecology: Endemic, known only from the type locality. Inhabits rocky and stony localities.

16. **Paronychia kurdica** Boiss. subspecies **haussknechtii** Chaudhri subsp. nov. (Plate VIII, Fig. 17).

Planta compacta, caespitosa, caulibus basi ramosissimis. Folia crassiuscula, 2–4 × 1–1.5 mm, anguste oblonga, obtusa, valde approximata-imbricata, plerumque velutino-pubescentia, sed ad apices ramulorum hirsuta. Capitula parva, 5 mm lata, sed copiosa, crebra et dense congesta. Bracteae ovatae, 2.5–3 × 2.5 mm, flores paulo superantes sed suboccultantes, circa flores convolutae. Flores oblongi, 2–2.5 mm longi, hirsutiusculi, sepala subinaequalia, exteriora breviter recurva. Fructus calycem replens, annulo collari pericarpii nullo.

Differt a *P. kurdica* Boiss. subsp. *kurdica* foliis valde imbricatis, bracteis parvis, sepalis subinaequalibus et breviter recurvatis, annulo collari pericarpium nullo.

Type: Turkey, "Syr. bor.", m. Saff Dagh. C. Haussknecht s. n., (JE), collected 27–6–1865.

Distribution and Ecology: Endemic in southern Turkey, northwest Syria, and Lebanon. Growing on limestone hills, screes, and rocks.

Paratypes: Turkey, Gaziantep. E. K. Balls, 2201 (E, S), 29–4–1935. M. Haradjian, 144 (G); 1253 (G, W, E), collected 6–1907. C. Haussknecht, S. N. (JE), 15–16–6–1865. Herb. Post, 260 (G), 3–6–1882; 4 (G), 6–1884.

Syria, Khan Assal (ad occident. ab Aleppo), Erik Wall, S. N. (S), 31–5–1933, alt. 360 m.

Lebanon, Stermal-Churbino, P. H. Davis, 5832 (E), 24–4–1943.

17. **Paronychia kurdica Boiss.** subspecies **montis-munzur** Chaudhri subsp. nov. (Plate VII, Fig. 18).

Planta laxe caespitosa. Internodia longa et pubescentia. Folia anguste oblongo-oblanceolata, basi attenuata, apice acuto, pilosa vel pubescentia-puberula. Bracteae ovato-acuminatae, flores superantes. Sepala anguste lanceolata, pilosissima, apice acuto-ciliata et valde recurvata.

Differt a *P. kurdica* Boiss. subsp. *kurdica* foliis acutis, sepalis anguste lanceolatis, acutis, et valde recurvatis.

Type: Turkey, Prov. Tunceli, Munzur Dagh, above Ovacik, alt. 1900 m. Davis and Hedge, D 31180 (U, holotype; E, isotype), collected 16–7–1957.

Distribution and Ecology: Confined to the central to north-central region of Turkey, from Munzur dagh to Nallihan west of Ankara. Growing on rocky limestone slopes, up to 1900 m.

Paratype: Kemaliye (Egin), P. Sintenis, 2323 (JE), in saxosis ad Euphratem, 20–5–1890.

18. **Paronychia kurdica** Boiss. ssp. kurdica var. **fragilis** Chaudhri var. nov. (Plate VII, Fig. 16).

A typo differt habitu fragilissimo, colore aureo-viridi.

Type: Prov. Ankara, above Tuz Gölü, 25 km north of Kochisar. McNeill, 326 (E), 29–7–1956, rock ledges, alt 900 m.

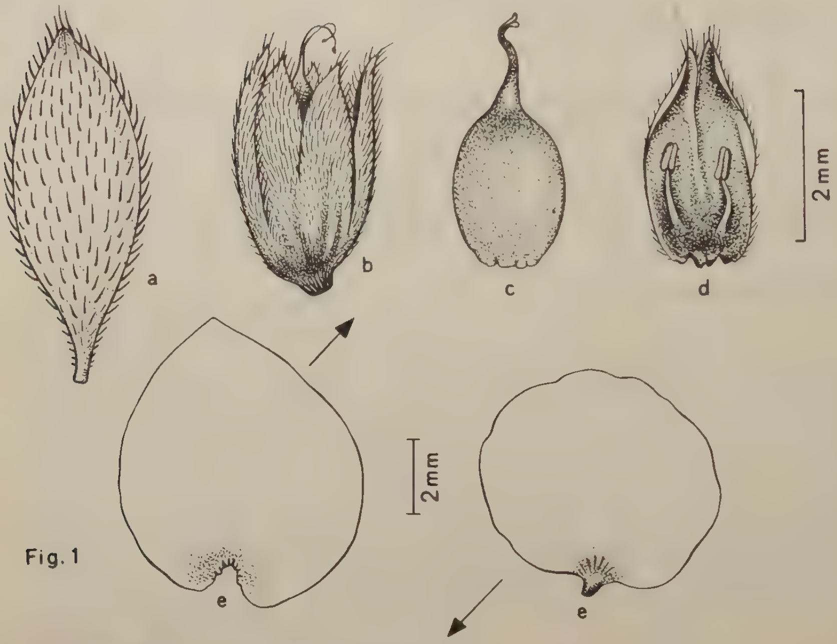

Fig. 1

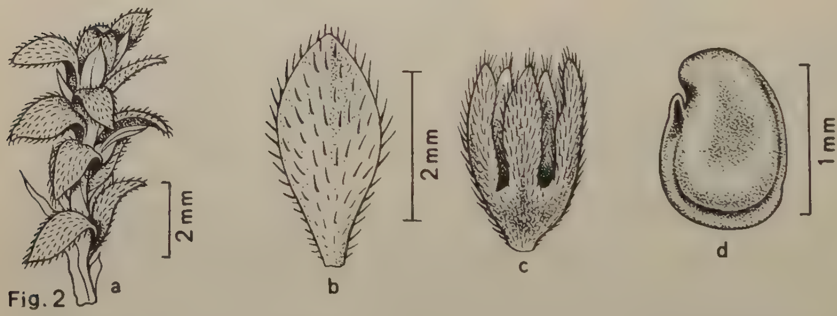

Fig. 2

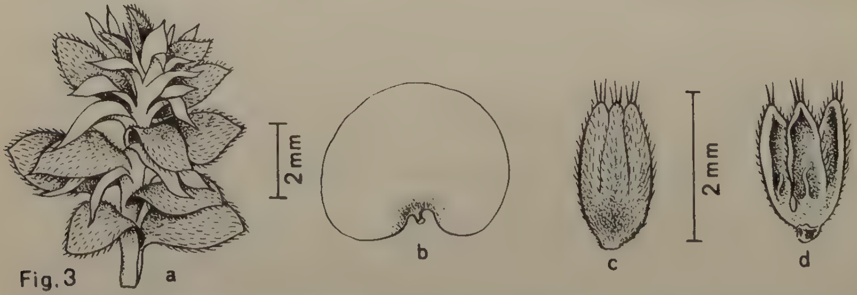

Fig. 3

Fig. 1. *Paronychia kotschyana*: a) leaf (× 10); b) flower (× 10); c) fruit (× 10); d) v.s. of flower (× 10); e) bract (× 5).

Fig. 2. *P. davisii:* a) shoot (× 5); b) leaf (× 10); c) flower (× 10); d) seed (× 5); e) bract (× 5).

Fig. 3. *P. lycica*: a) shoot (× 5); b) leaf (× 10); c) flower (× 10); d) v.s. of flower (× 10).

Plate I

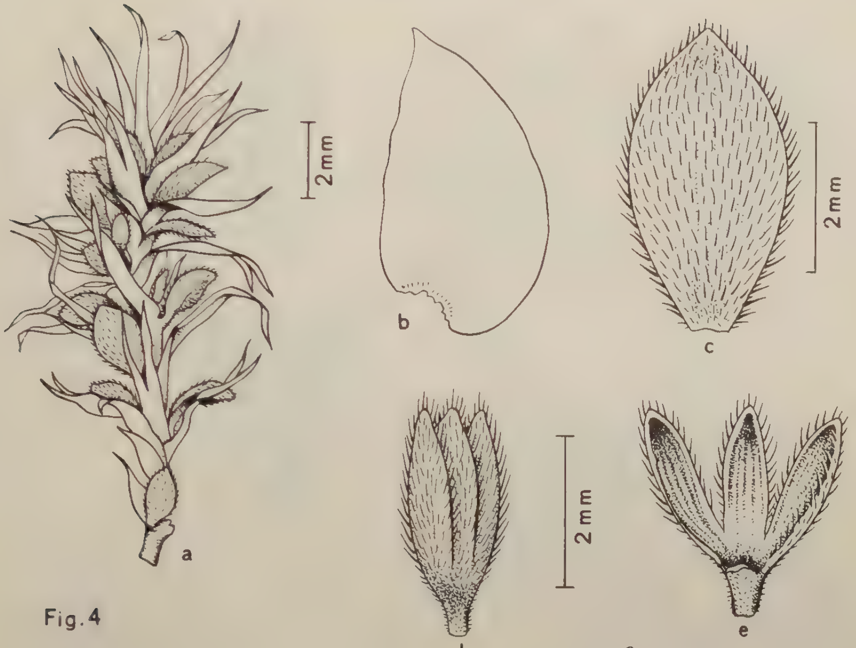

Fig. 4

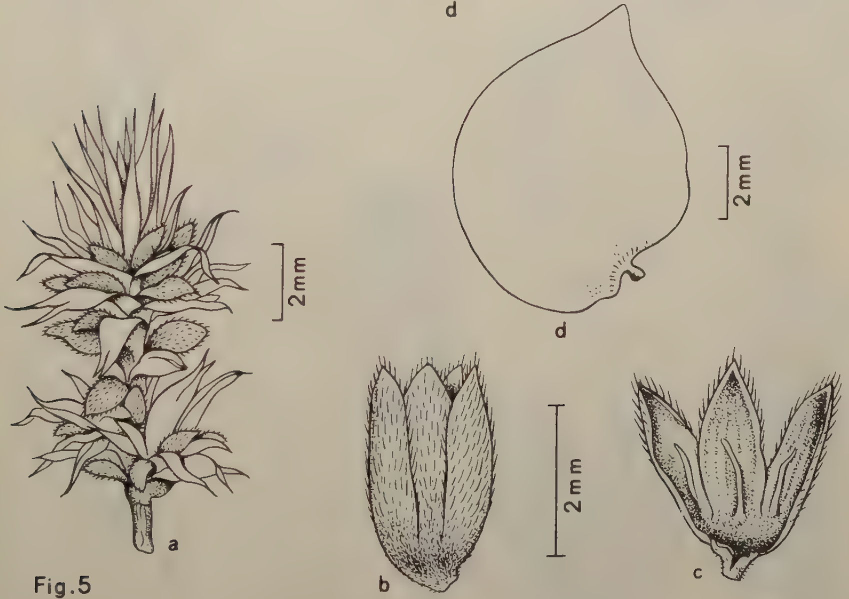

Fig. 5

Fig. 4. *Paronychia kemaliya:* a) shoot (× 5); b) bract (× 5); c) leaf (× 10); d) flower (× 10); e) v.s. of flower (× 10).

Fig. 5. *P. amani:* a) shoot (× 5); b) flower (× 10); c) v.s. of flower (× 10); d) bract (× 5).

Plate II

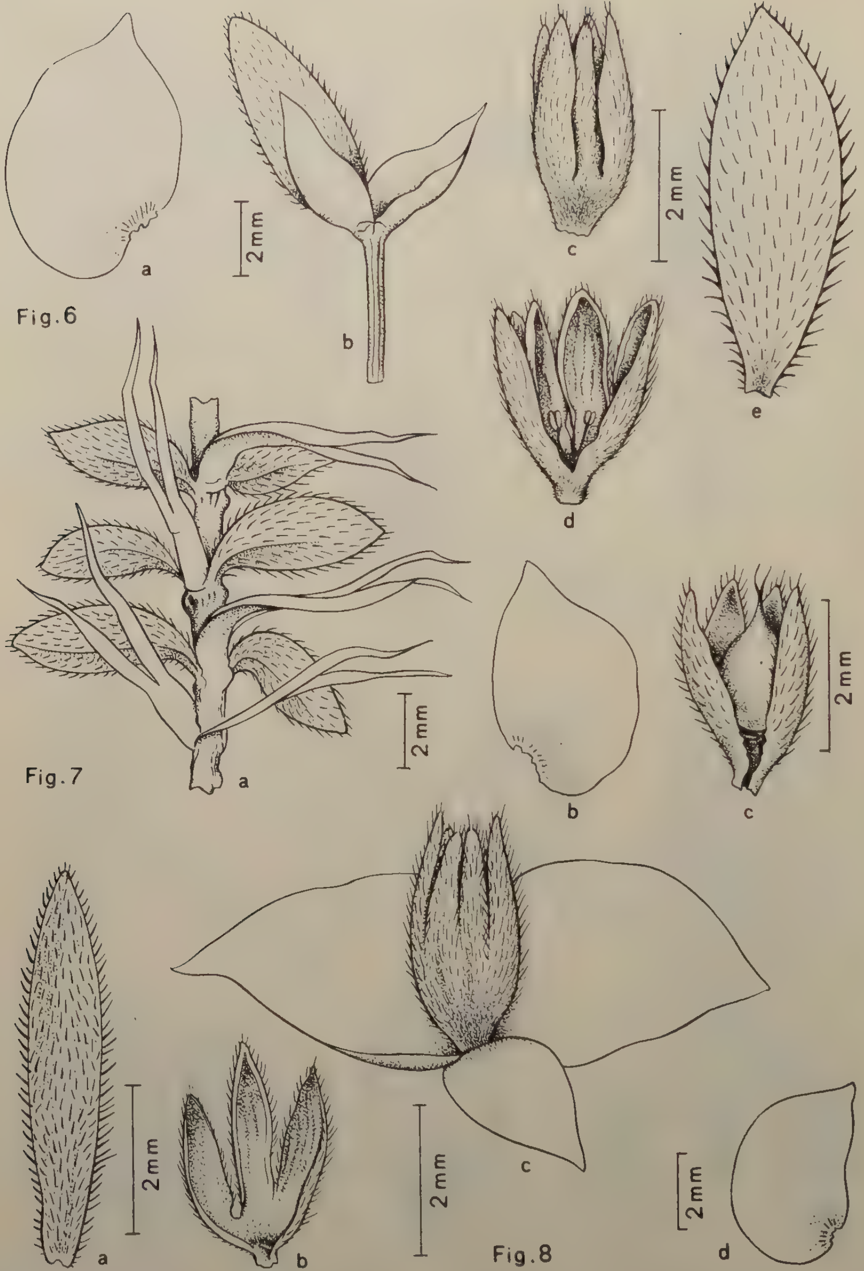

Fig. 6. *Paronychia paphlagonica:* a) bract (× 5); b) a part of shoot (× 5); c) flower (× 10); d) v.s. of flower (× 10); e) leaf (× 10).
Fig. 7. *P. cataonica:* a) shoot (× 5); b) bract (× 5); c) flower (dissected) (× 10).
Fig. 8. *P. dudleyi:* a) leaf (× 10); b) v.s. of flower (× 10); c) flower with bracts (× 10); d) bract (× 5).

Plate III

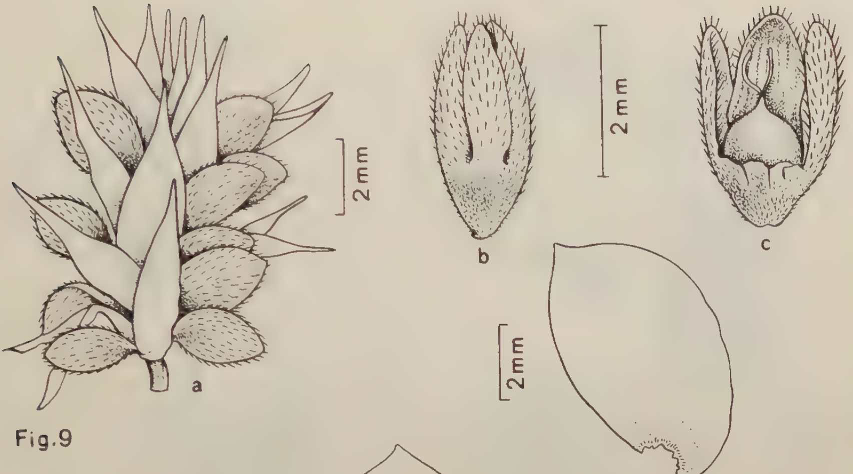

Fig.9

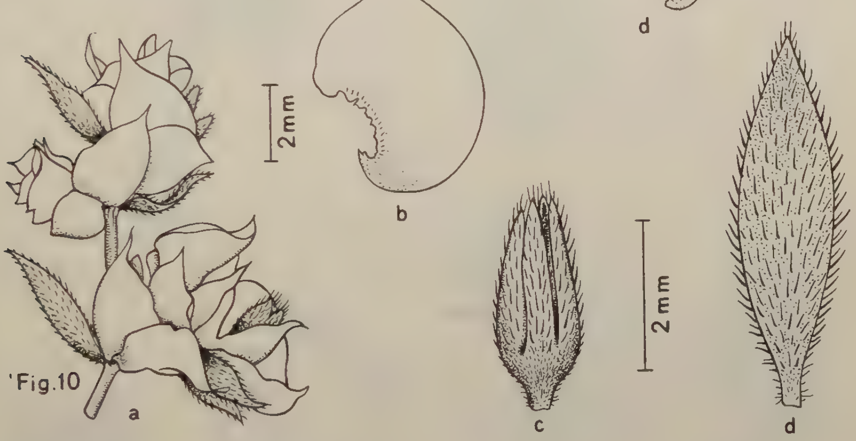

Fig.10

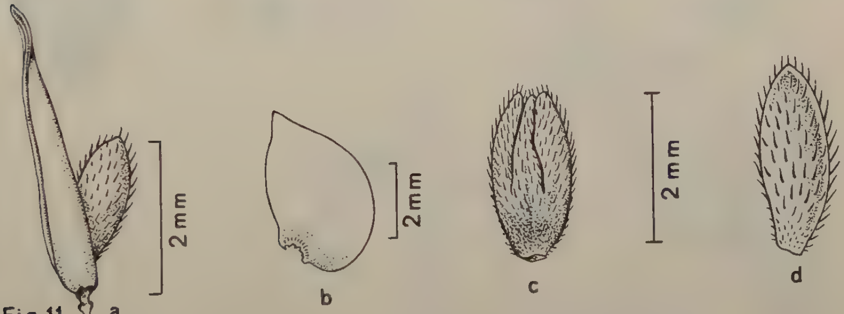

Fig.11

Fig. 9. *Paronychia turcica:* a) shoot (× 5); b) flower (× 10); c) v.s. of flower (× 10); d) bract (× 5).

Fig. 10. *P. galatica:* a) shoot (× 5); b) bract (× 5); c) flower (× 10); d) leaf (× 10).

Fig. 11. *P. condensata:* a) leaf with stipule (× 10); b) bract (× 5); c) flower (× 10); d) a leaf (× 10).

Plate IV

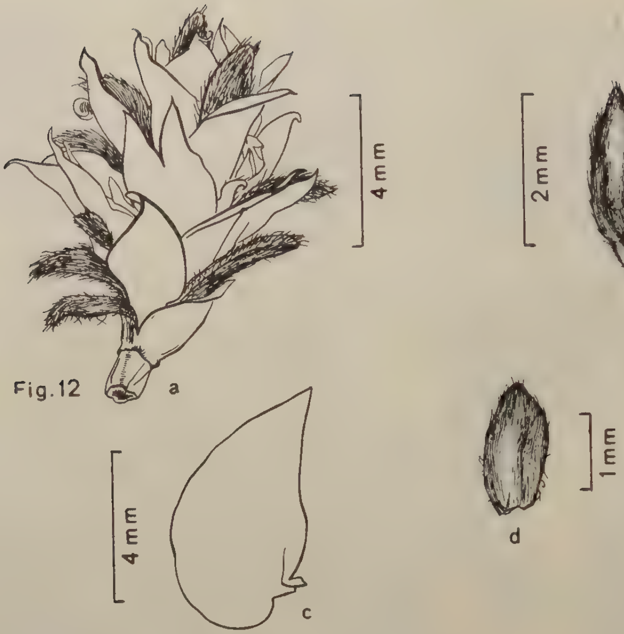

Fig.12

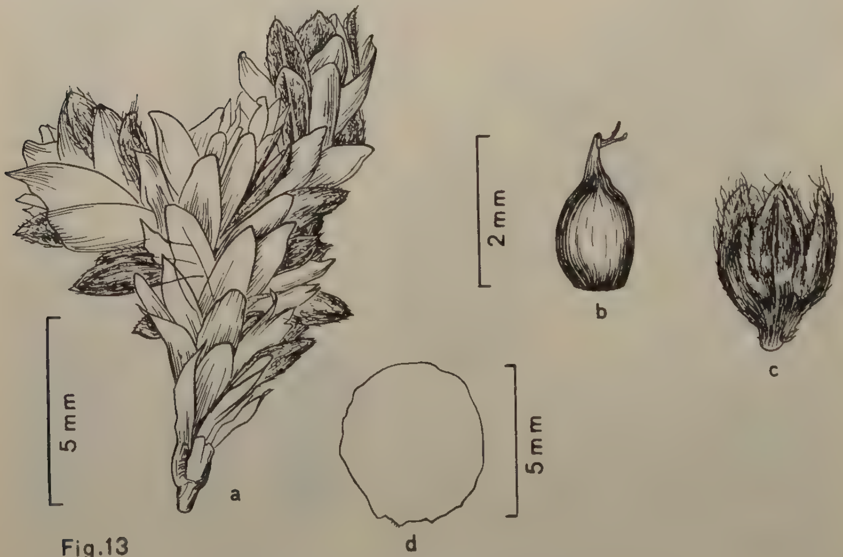

Fig.13

Fig. 12. *Paronychia angorensis:* a) shoot (× 5); b) flower (× 10); c) bract (× 5); d) leaf (× 10).

Fig. 13. *P. sintenisii:* a) shoot (× 5); b) fruit (× 10); c) flower (× 10); d) bract (× 4).

Plate V

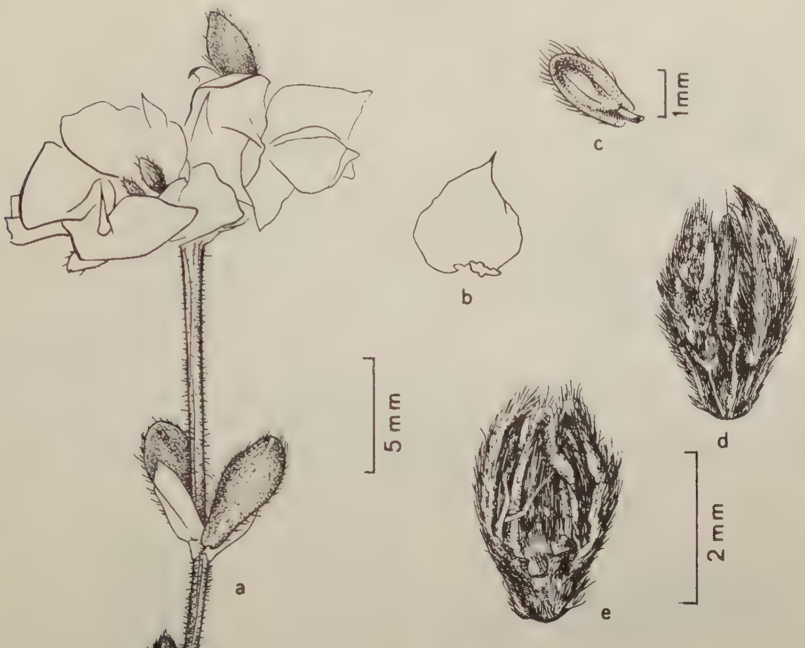

Fig.14

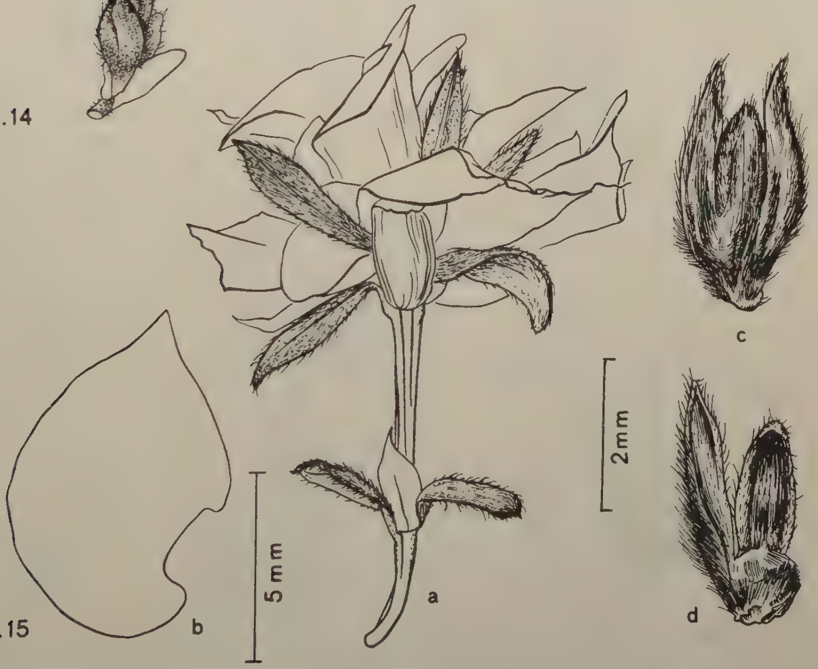

Fig.15

Fig. 14. *Paronychia mughlaei:* a) shoot (× 3); b) bract (× 3); c) leaf (× 6); d) and e) flower, outside and inside view (× 10).

Fig. 15. *P. carica:* a) shoot (× 5); b) bract (× 5); c) and d) sectional view of flower, outside and inside respectively (× 10).

Plate VI

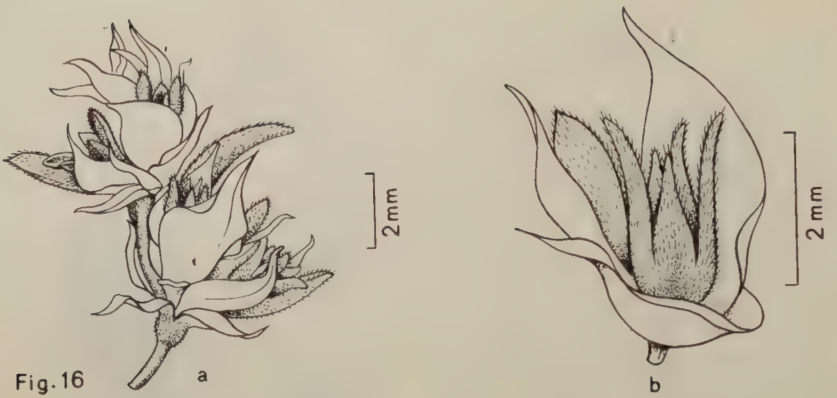

Fig. 16

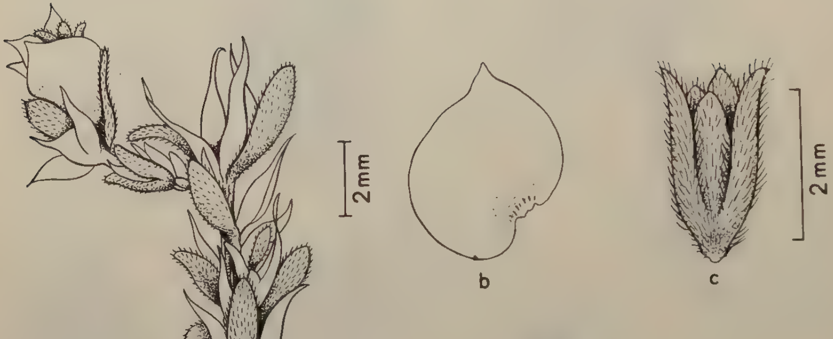

Fig. 17

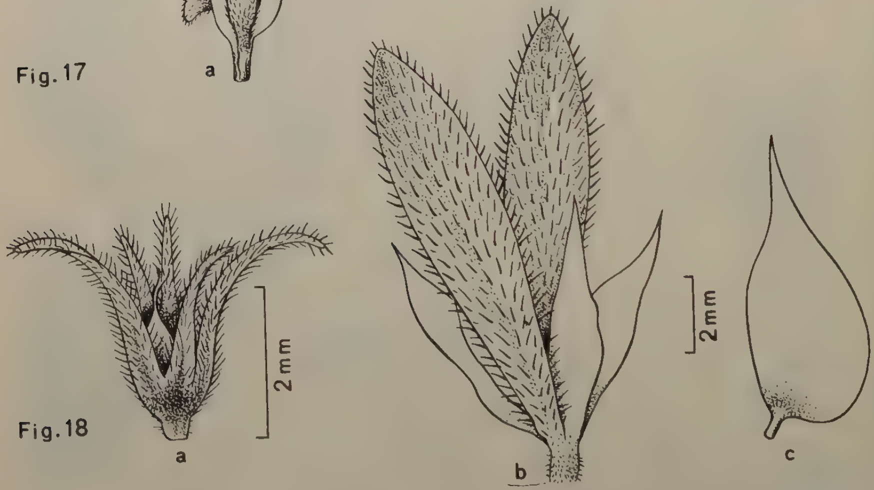

Fig. 18

Fig. 16. *Paronychia kurdica* Boiss., var. *fragilis:* a) shoot (× 5); b) a part of shoot (× 10).

Fig. 17. *P. kurdica*, ssp. *haussknechtii:* a) shoot (× 5); b) bract (× 5); c) flower (× 10).

Fig. 18. *P. kurdica*, ssp. *montis-munzur:* a) flower (× 10); b) leaves with stipules (× 5); c) bract (× 5).

Plate VII

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ALLANTOIN AND ALLANTOATE IN HIGHER PLANTS

CHR. VAN DER DRIFT and G. D. VOGELS

(Laboratory of Biochemistry, Nijmegen, the Netherlands)

(received October 1st, 1965)

ABSTRACT

The amounts of amide nitrogen, ammonia, allantoin and allantoate were determined in *Phaseolus hysterinus* Dur. and *Glycine hispida* L. during a growth period of 28 days. *P. hys.* grown under different conditions showed remarkable differences in the amount of allantoate. Allantoinase was present in both plants and some properties of the enzyme were described. Allantoate was broken down in *P. hys.* in a manner yet unknown.

1. INTRODUCTION

About the metabolic pathway of allantoin in higher plants still little is known. The conversion of allantoin into allantoate, a reaction catalyzed by the enzyme allantoinase (allantoin amido-hydrolase EC 3.5.2.5), has been found already in 1929 by FOSSE and BRUNEL in *Soja hispida*. This enzyme has been shown to be widely distributed in higher plants (TRACEY, 1955).

Allantoicase (allantoate amidinohydrolase EC 3.5.3.4), has been reported only once in higher plants (*viz.* in *Soja hispida* by ÉCHEVIN and BRUNEL, 1937).

This enzyme was supposed to catalyze the breakdown of allantoate into 2 moles of urea and 1 mole of glyoxylate. This conversion has now been shown to be a two-step reaction (TRIJBELS and VOGELS, 1966a).

Other pathways of allantoate degradation in plants have not been reported. The aim of our investigation was to study the enzyme allantoinase and to find out the pathway along which allantoate is degraded in plants.

2. MATERIALS AND METHODS

Preparation of plant extracts: *Phaseolus hysterinus* Dur. (*P. hys.*) and *Glycine hispida* L. "Tübinger" (soybeans) were grown in the greenhouse under constant illumination for 16 hours a day (4800 lux/cm^2). In some cases plants were grown in another way described in the text.

To prepare extracts plants were stored for one night at —20°C, thawed, cut into small pieces and ground in a chilled mortar with quartz sand in 0.05 M Tris-HC1 buffer, pH 7.4. The slurry was sonicated for 10 min in a MSE 500 W disintegrator and centrifuged at 10 000 g for 30 min. The cloudy supernatant was centrifuged at 100 000 g for one hour. The clear supernatant was used as enzyme source. In some experiments the residue obtained by centrifugation at 10 000 g was used as enzyme source. All operations during the preparation of the extracts were performed at 4°C.

Allantoin, allantoate, ureidoglycine, ureidoglycolate and glyoxylate were determined according to TRIJBELS and VOGELS (1966b). Amide nitrogen was determined as free ammonia after hydrolysis of a sample in 2 N HCl for 3 hours. Free ammonia was determined with Nessler reagent. 7-^{14}C-allantoin was prepared from K^{14}CNO and 5-aminohydantoin synthesized according to the method of BILTZ and GIESLER (1913).

Paperchromatography (descending development) was performed on Whatman No. 1 paper with phenol: water 4:1 (w/v) as solvent system. Allantoin, allantoate and urea were detected by spraying with p-dimethylaminobenzaldehyde in butanol: acetic acid 3:1. To detect radioactive compounds the dried chromatograms were passed through a Vanguard 880 automatic chromatogram scanner.

Allantoinase activity: the experiments were performed in mixtures containing per ml: 80 μmoles of TEA-HCl buffer, pH 7.4, 29 μmoles of allantoin, 0.3 μmoles of manganous sulphate and extract of soybeans or *P. hys.* containing 0.52 or 0.80 mg of protein, respectively. The mixtures were incubated at 30°C. The amount of allantoate formed was determined as described.

Unit of activity: one unit of allantoinase activity was defined as the amount, which will catalyze the transformation of 1 μmole of allantoin per minute under the conditions given. The specific activity was expressed in units per mg of protein.

Protein was determined according to LOWRY *et al.* (1951).

3. EXPERIMENTAL

The variation of some nitrogenous compounds during growth of *P. hys.* and soybeans was determined (Figs. 1 and 2). It appeared that amides and free ammonia were most abundant in *P. hys.*, whereas in soybeans only the amides were on a comparable level. Allantoin was present only in small amounts in both plants during all growth stages tested. Allantoate was present in moderate amounts; soybeans contained more allantoate than *P. hys.* In *P. hys.* the ammonia seems to be in contraphase with the amides and allantoate. During the test period we could never demonstrate the presence of urea.

From Table 1 it can be seen that plants grown in daylight on tap water contained more allantoate than plants grown under the same conditions on 0.5 % $(NH_4)_2SO_4$ in tap water. These plants contained also more allantoate than plants cultivated in the greenhouse. The greatest allantoate accumulation occurred when plants were grown in the dark on tap water.

In both plants allantoinase was present: *P. hys.* and soybeans contained 6.6 and 5.8 U/g of seed, respectively (specific activity 0.032 and 0.074 U/mg of protein). The total amount of allantoinase in each plant was constant during the tested period of 28 days. The pH-optimum of allantoinase from both sources was found to be 7.4.

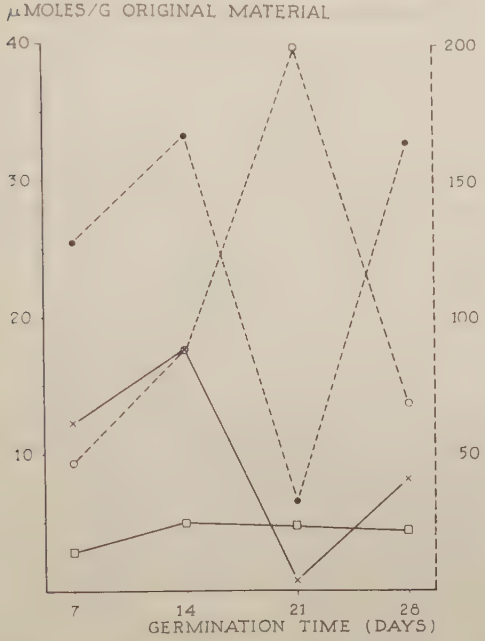

Fig. 1. Variation of some nitrogenous compounds during growth of *Phaseolus hysterinus:* allantoate (×———×), allantoin (□———□), amide nitrogen (●– – – –●) and NH_3 (○– – – –○).

The allantoinase reaction was completely inhibited by cysteine in a concentration of 8 mM. Phosphate ions too had an inhibiting effect on the enzymic activity. This is in accordance with the result found by LEE and ROUSH (1964). The K_m-values of the allantoinases from *P. hys.* and soybeans are 4.6×10^{-2}M and 1.4×10^{-2}M, respectively.

In contrast to the results of LEE and ROUSH (1964), who found an absolute specificity of the enzyme from soybeans for d-allantoin, we could not demonstrate such a specificity of the enzyme from both plants for d-allantoin, although optical rotation studies showed that in the case of soybean allantoinase d-allantoin was broken down about 10 times more rapidly than the l-form (Fig. 3). Manganous ions had only a slight activating effect on soybean allantoinase; the activity of allantoinase from *P. hys.* was not influenced by these ions.

On incubation of 25 mM sodium allantoate in 0.1 M phosphate buffer, pH 7.4, with the *P. hys.* residue at 30°C about 15 % of the substrate disappeared within one hour. Upon prolonged incubation up to 24 hours only 25–30 % of the substrate disappeared. However, we could not demonstrate the production of ureidoglycine, ureidoglycolate, glyoxylate or ammonia, which should be produced when allantoate was broken down according to one of the pathways known at this moment (VOGELS, 1966). After 24 hours of incubation only urea was found. Its presence has been demonstrated by paper-

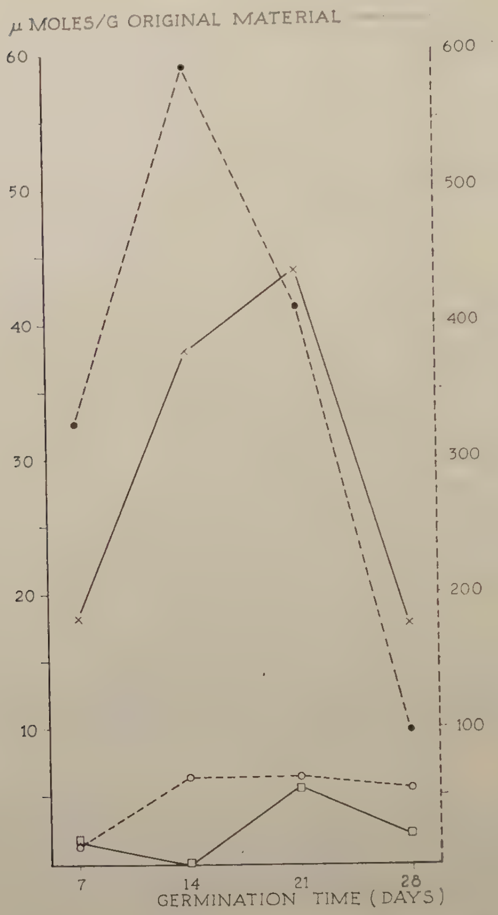

Fig. 2. Variation of some nitrogenous compounds during growth of *Glycine hispida:* allantoate (×———×), allantoin (□———□), amide nitrogen (●– – – –●) and NH_3 (⊙ – – – – ○).

TABLE 1

Amount of Allantoate present in *Phaseolus hysterinus* grown under different conditions

	Allantoate (µmoles/g original material)			
Germination time (days)	Daylight (tap water)	Daylight (0.5% $(NH_4)_2SO_4$)	Dark (tap water)	Greenhouse
3	10	11.5	16.1	—
6	15.7	13.5	22.5	—
9	29.7	19.5	—	13.9
15	52	31.2	—	15.2

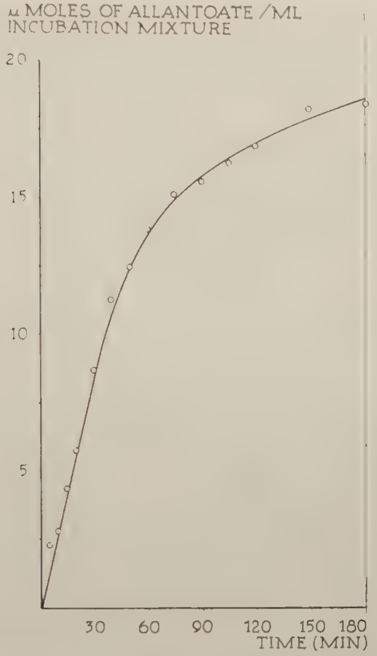

Fig. 3. Allantoate formation from allantoin by allantoinase from soybeans. Experiments were performed as described under Materials and Methods.

chromatography of an aliquot of the incubation mixture. On addition of urease to an aliquot of the incubation mixture ammonia was formed and after chromatography no urea could be detected.

Under similar conditions 7-^{14}C-allantoin was incubated: after 2, 4, 6 and 24 hours of incubation a 20 μl aliquot was taken and subjected to paperchromatography. After drying the paperstrips were scanned for radioactivity. In this case after 24 hours of incubation also only urea was found, outside allantoin and allantoate.

In soybeans we did not observe any disappearance of allantoate, under the same conditions. When the 100 000 g supernatant was used as enzyme source no disappearance of allantoate occurred in both plants.

4. Discussion

Plants grown in the dark show a much greater allantoate accumulation than plants grown in daylight or constant illumination. A similar effect was observed for *Soja hispida* (Échevin and Brunel, 1937) and *Trifolium sativum* (Fosse, de Graeve and Thomas, 1933). So, there may be some connection between allantoate degradation and photosynthesis. In agreement with this Reinbothe (1961) suggested that in chlorophyll-deficient leaves an allantoate degrading enzyme activity was absent. This hypothesis shall need further work to confirm this point of view.

Allantoinase is in higher plants a constitutive enzyme. The specific activity of allantoinase in our crude extracts of *P.hys.* and soybeans is much greater than that found for allantoinase from soybeans and mung beans (LEE and ROUSH, 1964; NAGAI and FUNAHASHI, 1961).

ACKNOWLEDGEMENTS

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Acta Botanica Neerlandica **15** (1966) 215–223

EFFECT OF 2-THIOURACIL AND GIBBERELLIC ACID ON FLOWER FORMATION IN WEDGWOOD IRIS

A. S. RODRIGUES PEREIRA

(Department of Botany, University, Nijmegen, the Netherlands)

(received October 1st, 1965)

Abstract

1) 2-Thiouracil (2-TU) applied during low temperature treatment, inhibited flower formation in excised stem discs of Wedgwood iris. The inhibition was overcome by gibberellic acid (GA) and orotic acid but not by uracil or thymidine.

2) The first signs both of an inhibitive effect on flower initiation by 2-TU and of GA promotion occurred at the beginning of the reproductive stage. Increase or decrease of the rate of development of the flower primordium could be established only two weeks later, during differentiation of stamens or tepals.

3) The peak in respiration rate occurring in the bud at the beginning of the reproductive stage was entirely repressed by 2-TU and not restored on a medium containing 2-TU and GA.

4) It is concluded that a specific RNA takes part in the earlier stages of flower formation in Wedgwood iris.

5) The role of gibberellin-like substances in flower formation of the Wedgwood iris is discussed in the light of possible interaction with nucleic acid metabolism.

Introduction

Expression of the floral stimulus in photoperiodically sensitive plants is affected by compounds that are known to hamper nucleic acid synthesis (Collins, Salisbury and Ross, 1963). The inhibition of flowering in *Streptocarpus* by 2-thiouracil (2-TU) (Hess, 1959), in *Pharbitis nil* by 8-azaguanine (8-Az) and 2-TU (Marushige and Marushige, 1962), in *Cannabis sativa* by 2-TU (Heslop-harrison, 1960) and in *Xanthium* by 5-fluorouracil (5-FU) (Salisbury and Bonner, 1960; Bonner and Zeevaart, 1962) seems to involve inhibition of synthesis of ribonucleic acid (RNA). According to Zeevaart (1962) inhibition of flowering in *Pharbitis nil* by 5-FU and 5-fluorodeoxyuridine involves inhibition of synthesis of deoxyribonucleic acid (DNA) and of cell multiplication in the apex. Brown (1962) found promotion of flower formation after application of iododeoxyuridine to the axils of *Arabidopsis* seedlings (which is a facultative LDP). It may therefore be asked whether flower formation in photoperiodically non-sensitive plants can also be influenced by these antimetabolites. Stem disc cultures of Wedgwood iris bulbs seem suitable objects for study of this point, especially since, according to Zeevaart (1962) it is the realization of the flowering stimulus in the apex and not its production in the leaf that seems to depend on nucleic acid metabolism.

Gibberellic acid (GA) is known to promote flower formation in LDP's and in cold requiring plants (Lang and Reinhard, 1961). In Wedgwood iris, induction and differentiation of flower primordia takes place at 13°, and both in the bulb and the excised bud this process is promoted by GA (HALEVY and SHOUB, 1964; RODRIGUES PEREIRA, 1962, 1965). ZEEVAART (1962) found that inhibition of flower formation in *Pharbitis nil* by 5-FU could not be reversed by application of GA.

In the present series of experiments the antimetabolites 8-azaguanine, 5-fluorouracil or 2-thiouracil, alone or combined with the metabolites guanine, uracil, kinetin, orotic acid, thymidine or gibberellic acid were applied to excised stem discs of Wedgwood iris cultured on a nutrient medium and their influence on flower formation in the bud studied.

MATERIAL AND METHODS

All experiments were carried out with buds taken from large bulbs of *Wedgwood iris* possessing 100%flowering capacity. Methods for isolating and culturing explants were described earlier (RODRIGUES PEREIRA 1962, 1964), but may be briefly summarized here.

Before isolating the stem discs, bulbs were partially induced at 13°, with the duration of this induction (= pretreatment) depending on time of the year. Standard nutrient medium consisted of Knop's solution half strength, Heller's micronutrient solution, sucrose and agar. The explants were either cultured on the standard medium to which the compounds to be tested were added before autoclaving, or they were dipped into autoclaved aqueous solutions of these compounds and afterwards cultured on the standard medium. The amount of solution being brought on the explants by the latter procedure was 38.8 ± 4.2 mg. Although this method has the advantage of greater simplicity, incorporation of the chemical into the medium was more effective and the results were less variable. The 5-fluorouracil was kindly supplied by Hoffmann – La Roche, Basel, Switzerland; the gibberellic acid by Plant Protection Ltd., Yalding, Kent, England.

Respiration measurements were carried out using a standard Warburg apparatus following procedures described earlier (RODRIGUES PEREIRA 1962). This part of the experiments was conducted by Mr. O. Th. Schönherr.

Most of the experiments were carried out at least three times; there was an average of at least 20 explants per treatment.

RESULTS

1. *Preliminary experiments*

In experiments that were not followed up further the activity of 8-Az and 5-FU as inhibitors of flower formation and the ability of guanine and kinetin, and of thymidine, orotic acid and gibberellic acid to counteract this inhibition were tested.

Depending on concentration, both compounds had an adverse effect on flower formation. Although also at lower concentrations a small effect was noted, inhibition only became evident at 10^{-4} M, which concentration, however, was already a little toxic. Therefore, it does not seem probable that the two compounds are acting as specific inhibitors of flower formation in iris.

In concentrations rangeing from 10^{-6} to 10^{-4} M, neither of the four metabolites applied showed any consistent effect.

There were small indications that inhibition by 8-Az was counteracted by kinetin and guanine, and 5-FU inhibition by orotic acid and thymidine. Inhibition by 5-FU was in one experiment partly and in another one entirely overcome by gibberellic acid (Table 1).

In direct mutual comparison of the activities of orotic acid and GA as combined with the antimetabolite, it was established that reversal by GA was more pronounced.

TABLE 1

Ability of different metabolites to antidote 5-FU inhibition of flower formation in excised stem discs of Wedgwood iris

chemicals applied	flower formation					
	series I			series II		
	n_t	n_r	score	n_t	n_r	score
control	48	34	5	43	31	5
5-FU 3 × 10^{-5} M	22	0	—	24	14	5
5-FU 3 × 10^{-5} M + orotic acid 10^{-4} M	24	10	3	24	10	3
5-FU 3 × 10^{-5} M + thymidine 10^{-4} M	20	5	3	24	3	2
5-FU 3 × 10^{-5} M + GA 10^{-4} M	19	14	3	24	19	5

Chemicals incorporated into the medium. Pretreatment of bulbs of series I 2 weeks at 13°, of series II 10 days at 13°. Duration of experiment (pretreatment of bulbs plus incubation of buds) 7 weeks. n_t = number of stem discs incubated; n_r = number of apices found reproductive at control; score = average stage of flower formation in reproductive apices expressed in equal units ranging from 0–14.

2. *2-Thiouracil and gibberellic acid*

In our experiments the antimetabolite 2-TU was a more effective inhibiting agent than 5-FU. In one series of experiments 2-TU was tested over a range of concentrations, up to 10^{-3} M in trials with nutrient media containing pre-added 2-TU and up to 10^{-2} M in dipping experiments. In four out of six experiments, one of which is presented in Table 2, inhibition increased generally with concentration. In one dipping experiment in which the buds were only slightly activated at the outset and, by consequence, score in the flower forming controls was low, the lowest concentration applied caused an increase instead of a decrease; in another experiment the

TABLE 2

Effect of 2-thiouracil on flower formation in excised buds of Wedgwood iris

concentration of inhibitor	flower formation		
	n_t	n_r	score
control	21	21	9
2-thiouracil 10^{-4} M .	23	21	8
5 × 10^{-4} M	20	18	6
10^{-3} M	23	20	4
2 × 10^{-3} M	44	13	4
4 × 10^{-3} M	22	0	—

Dipping experiment; pretreatment of bulbs 2 weeks at 13°; duration of experiment 6 weeks. Other data as in Table 1.

lowest inhibiting concentration was as high as 2 × 10^{-3} M. In four out of six experiments in which several 2-TU concentrations were used, and in six out of ten experiments with one concentration, 2-TU inhibition of flower formation could be proved statistically.

Inhibition by 2-TU was not reversed by uracil or thymidine; it was, however, by orotic acid and GA (Tables 3 and 4). In several experiments the effect of 2-TU doses capable of depressing both n_r and score was reversed by equal (or slightly higher) concentrations of GA or orotic acid. In four out of four experiments, using various concentrations, number of reproductive apices was greater at combinations of 2-TU and GA, than when the inhibitor alone was applied. In three experiments with weekly sampling, using selected concentrations of 2-TU and GA (see next paragraph) n_r was twice and score once found higher with 2-TU and GA together than with the single inhibitor. With orotic acid no linear dependency on concentration

TABLE 3

Ability of orotic acid and gibberellic acid to antidote 2-thiouracil inhibition of flower formation in excised buds of Wedgwood iris

exp. nr.	chemicals applied	flower formation		
		n_t	n_r	score
1	control.	34	27	5
	2-TU 10^{-3} M	18	9	3
	2-TU 10^{-3} M + orotic acid 10^{-3} M	18	17	5
2	control.	14	11	5
	2-TU 2 × 10^{-3} M	47	10	3
	2-TU 2 × 10^{-3} M + GA 10^{-3} M	24	14	4

Dipping experiments. Exp. nr. 1: pretreatment 3 weeks at 13°; exp. nr. 2: pretreatment 1 week at 13°. Other data as in Table 1.

TABLE 4

Influence of 2-thiouracil and gibberellic acid on flower formation in excised stem discs of Wedgwood iris

concentration of gibberellic acid	flower formation					
	gibberellic acid			3 × 10^{-5} M 2–TU + gibberellic acid		
	n_t	n_r	score	n_t	n_r	score
	48	34	5	24	1	3
3 × 10^{-6} M	22	16	4	23	6	3
10^{-5} M	23	16	5	24	4	2
3 × 10^{-5} M	24	19	5	24	6	3
10^{-4} M	24	21	7	23	12	4
3 × 10^{-4} M	23	22	8	24	0	—

Chemicals incorporated into the medium. Pretreatment 2 weeks at 13°. Duration of experiment 7 weeks. Other data as in Table 1.

could be established. Very high amounts of GA sometimes did not reverse 2-TU inhibition at all, whereas in the same experiment low amounts did. Gibberellic acid applied alone never became inhibitory, even at high concentration.

By investigating several samples at intervals of 1 or 2 weeks following the start of the incubation, it was tried to find out whether susceptibility of stem discs to the activities of 2-TU, GA or the two together is dependent on time (Table 4). For example, the first sign of inhibition by 2-TU was found 4 weeks after the beginning of the experiments (i.e. after one week of bulb pretreatment and three weeks incubation). At that time the controls had just entered the first stage of the reproductive primordium (stage II, according to BEYER, 1942). Also after four weeks on the medium containing GA, n_r was slightly increased. One week later there was still no difference in score between the controls and the 2-TU and GA treated stem discs respectively. Six weeks after the beginning of the experiments score in the 2-TU treated stem discs was clearly depressed, whereas on the GA containing medium it was as clearly increased.

TABLE 5

Influence of 2-thiouracil and gibberellic acid on the flower formation in excised buds of Wedgwood iris

chemicals applied	flower formation								
	4 weeks			5 weeks			6 weeks		
	n_t	n_r	score	n_t	n_r	score	n_t	n_r	score
control	15	7	3	14	8	3	14	11	5
GA 10^{-4} M	15	11	3	13	11	4	14	12	10
2-TU 3×10^{-5} M	13	0	—	12	2	3	13	7	5
2-TU 3×10^{-5} M + GA 10^{-4} M	13	2	3	13	3	4	12	6	10

Pretreatment of bulbs 1 week at 13°. Chemicals incorporated into the medium. Three weeks after the beginning of the experiment the buds were still vegetative. Other data as in Table 1.

3. *Respiration measurements*

They were carried out with standard Warburg apparatus, using the methods described earlier. Excised stem discs were incubated on standard nutrient agar to which 2-TU, GA or both were added. At one-week intervals oxygen uptake of 5 of them together was measured in triplicate at 20°, in a solution containing the anorganic macronutrients of the standard medium. There were 0.2 ml 10 % NaOH and a wick in the side arm. After the manometric measurements were completed, developmental stages of the apices were determined (Table 4) and the explants discarded. Bulbs were pretreated by holding them at 13° for one week. The first measurements were carried out one week after the beginning of the incubation period, at which time all buds were still vegetative. Figure 1 gives the time course of respiration intensities over the experimental period.

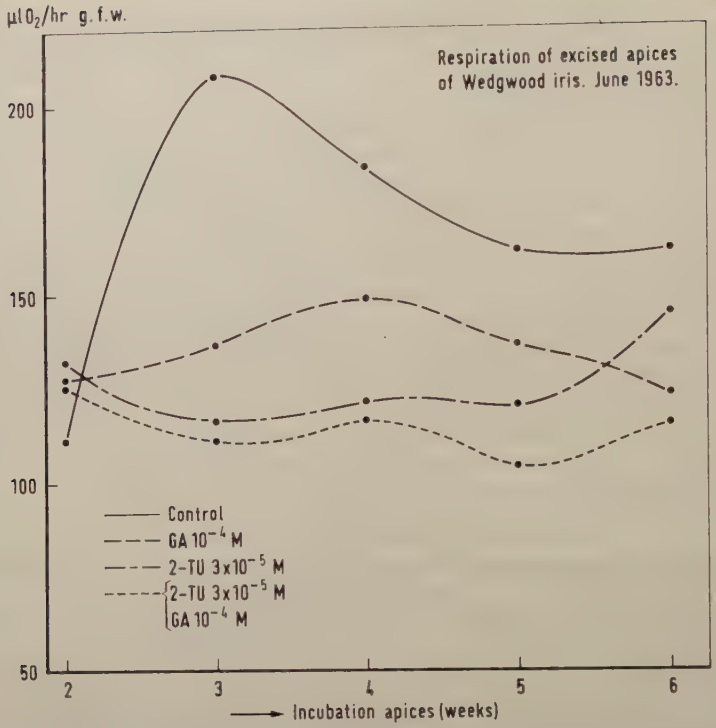

Fig. 1. Influence of 2-thiouracil and gibberellic acid on time course of respiration rate of excised stem discs during flower formation at 13°. Same buds as in Table 5. See data.

Plotting respiration rates of buds of iris bulbs incubated at flower forming temperature against time gives a characteristic maximum at the beginning of the reproductive stage (Rodrigues Pereira, 1962), whether measurements are carried out at this same temperature or at 20°. A similar peak is seen when developmental stage (time) is plotted against respiration rate of excised stem discs incubated on a nutrient medium, both with and without exogenous GA. GA lowers respiration rate and 2-TU depresses it even more, and moreover 2-TU treatment results in the disappearence of the peak at the transition to the reproductive stage. Although 2-TU inhibition of flower formation is to a considerable extent reversed by GA, on the medium containing both 2-TU and GA respiration rate is about equal to that on the 2-TU medium, nor has the peak been restored.

Discussion

There are some differences between the object of our investigations and those of the pertinent experiments described in the literature. The latter, *Cannabis*, *Streptocarpus*, *Xanthium*, *Pharbitis*, are all photoperiodically sensitive plants; antimetabolites were applied to the leaf or the bud during or after induction in order to analyse their effect on induction or on realization of the flowering stimulus in the apex. Flower formation in Wedgwood iris bulbs is temperature induced, in the excised stem disc the leaves are absent and on media without any flowering agent added there is no matter of transport. In isolated scale fragments incubated on a nutrient medium, the contents of certain growth substances increase at the temperature which is optimal for flower formation, and we are probably entitled to make the same assumption for the bud. It follows that increase of these compounds in the bud of the normal bulb, as it was established in an earlier publication (RODRIGUES PEREIRA, 1964) may not be entirely caused by transport from the scales; on the contrary it is shown here that the whole process of flower formation can take place in the single apex.

The present results are in agreement with those reported by SALISBURY and BONNER (1960) and BONNER and ZEEVAART (1962) who showed that floral induction in Xanthium can be suppressed by 5-FU and that this suppression is reversible by orotic acid. From the present study it is evident that thymidine and GA are also capable of suppressing 5-FU induced inhibition.

In Wedgwood iris combinations of 2-TU with orotic acid or with gibberellic acid reveal much more about floral inhibition and its reversal. As is the case with 5-FU, 2-TU may in principle be supposed to interfere with DNA and/or RNA synthesis. The research of HESS (1961) has established that 2-TU inhibition of flowering in *Streptocarpus wendlandii* may be attributed to interference with synthesis of a specific flower-forming RNA. However, it does not seem to be established that 2-TU, as applied in his experiments, did not have an effect on vegetative growth. MARUSHIGE and MARUSHIGE (1962) have even pointed out that in their experiments on *Pharbitis nil* vegetative and flowering effects are unseparable. In our experiments with various antimetabolites the higher concentrations appeared to be toxic and even lethal, which might suggest that the harmful processes concerned also occur to some extent at lower concentrations.

The results of our respiration measurements, however, clearly suggest a specific action. The respiration rate in stem discs incubated on a 2-TU containing medium being depressed during the whole of the experimental period may be due to a general metabolic effect; but the total disappearance of the peak at the commencement of the reproductive stage suggests that at this time a much greater part of the respiration rate is inhibited than at any other time during the course of flower formation. Therefore, it may be deduced that at least at this developmental stage a specific 2-TU inhibitable nucleic acid activity is expressed as an increase in rate of respiration. Although the accompanying deceleration in flower formation is nullified by GA, the respiratory activity of this specific nucleic acid is evidently not restored. So perhaps we may conclude that there is only a very indirect relationship between the transition to the reproductive stage and the rise in respiration rate occurring at the same time.

Although the activity of 2-TU seemed to be more readily on the transition to the reproductive stage, whereas the effect of GA was more pronounced in the rate of development of the flower primordium, yet in either case it was impossible to differentiate between the two effects. On the other hand it does not seem warranted to measure progress in flower formation by one parameter, being a combination of n_r and score, because at the succeeding stages different mechanisms may be at work.

In examining the results of the present series of experiments it appears that also in cold requiring species such as Wedgwood iris it is possible to interfere with flower formation by way of inhibitors of nucleic acid metabolism. Although inhibition of flower formation by these substances and its reversal by GA has been established, we might not suggest that there is any direct interaction of GA with the metabolites concerned. The same inference can be drawn from the work by Zeevaart (1962) and Brown (1962) on interaction of GA and DNA metabolism in flower formation of *Pharbitis* and *Arabidopsis*. Evidence is accumulating, however, that several growth promoting activities of GA are exerted by way of its more or less directly interfering with nucleic acid metabolism. Activities of a variety of enzymes (amylases, protease, catalase, cellulase, phosphatase) are shown to be stimulated by gibberellic acid (Dahlstrøm and Sfat, 1961). These authors suggested that the mechanism of the stimulation of these various enzyme systems occurs on the level of enzyme synthesis. Sahai Srivastava and Meredith (1962) found that in germinating barley kernels amylase activity is depressed under the influence of chloramphenicol sodium succinate (CAL) which is thought to interfere with the function of the RNA component concerned in amino acid incorporation into proteins. In a solution containing CAL and GA this activity is not only restored but it is much greater than in water and almost as great as in GA alone. In our laboratory similar results were obtained by Schönherr (unpublished) with growth of lettuce seedling hypocotyls, which is known to be specifically increased by GA (Frankland and Wareing, 1960). Schönherr found that growth of lettuce seedling hypocotyls was inhibited by CAL and by 2-TU and that in solutions of GA and any of the inhibitors, depending on the concentration ratio growth exceeded that in water.

Lastly, from recent investigations by Masuda and coworkers (Masuda and Yanagishima, 1965) it also appears that GA exerts its growth promoting activities in Jerusalem artichoke, the *Avena* coleoptile and certain yeast strains, by way of a specific RNA.

Therefore, although no interaction could be established between GA and any of the metabolites used so far in the various investigations discussed, it seems justified to conclude that there are definite and even several points of contact between GA metabolism and nucleic acid metabolism. By way of these points of contact endogenous and exogenous gibberellin-like growth substances may influence such diverse processes as germination, elongation and flower formation. Added to this in the case of flower formation, and probably in all cases, is the time dimension through which successive partial processes are controlled by different growth substances that in turn might be different forms of the same basic substance.

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THE SYSTEM OF THE ORCHIDALES

P. VERMEULEN

(Hugo de Vries Laboratorium, Amsterdam)

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Abstract

After an enumeration of the most characteristic features of the *Orchidales*, the affinities between this order and other monocotyledonous groups are discussed. The *Orchidales* must be placed in the system immediately after the *Commelinales*, chiefly on account of their androecial morphology. For reasons explained in the present paper the *Orchidales* are subdivided into three families, viz. the *Apostasiaceae*, *Cypripediaceae* and *Orchidaceae*. The principal differences between these families are shown in the form of tables.

In the *Orchidaceae* two subfamilies are recognised and amply circumscribed, viz., the *Orchidoideae* and the *Epidendroideae*, the latter again being subdivided into the two contribes *Neottianthae* and *Epidendranthae*.

The androecial morphology is discussed in detail in connection with atavistically developed stamens, with the presence of staminodes (or supernumerary stamens) and with the floral morphology of certain taxa. The auricles are not regarded as staminodes because they persist in flowers with supernumerary (atavistically re-appeared) stamens and also because they lack vascular bundles. The gynostemial wings in some Australian genera (*Diuris*, *Prasophyllum*, and other ones) are considered to be of androecial derivation The less conspicuously winged but vascularised margins of the gynostemium of many *Epidendroideae* likewise represent androecial elements incorporated in the column.

The suggestion, made by E. Nelson, that the lip is the phylogenetic derivative (the homologue) of the 'missing' stamens A_2, a_3 and A_3 (which implies that the median petal has disappeared), is rejected, primarily because Nelson's arguments are based on the morphology of the labellum in the highly specialised genus *Ophrys*. The floral morphology of *Neuwiedia* and of some species of *Herminium*, on the contrary, is indicative of the petaloid nature of the lip which, accordingly, represents the median petal. The vascular anatomy of the orchid flower does not provide arguments in favour of the suggestion made by Lindley (later taken up by Darwin) that the 'missing' stamens A_2 and A_3 are incorporated in the gynostemium.

The orchidalean ovary appears to be compounded of six parts, viz. three broad hyposepalous zones alternating with as many hypopetalous elements bearing the (double) laminal placentae on their inner face. This is considered to be a convergence towards the condition prevailing in *Rhoeadales (Brassicales)* (genus *Eschscholzia* etc.).

In the *Orchidoideae* the stigma is locally differentiated into viscid discs which are situated distally of the lateral stigmatic lobes, and the median stigmatic lobe is functional in several genera, but in the *Epidendroideae* the median stigmatic lobe is apically transformed into a mucilaginous substance or a viscid disc, or it is completely replaced by a viscidium. In *Stereosandra* the viscidial element is a derivative of the anther.

1. Historical introduction

In his Systema Naturae (1735), Linnaeus distinguishes as Classis XX the *Gynandria* ("Stamina pistillis (non receptaculo) insident"), to which he refers various groups, viz. the *Diandria*, being the orchids including, e.g., *Orchis* and *Cypripedium*, the *Triandria* with *Sisyrinchium*, the *Tetrandria* with *Nepenthes*, etc. Linnaeus apparently regarded the pollinia as stamens. ADANSON, in his Familles des Plantes (II, 1763), described "*Les Orchis*" as having only one stamen, but he also classified *Cypripedium* among this group. Olof SWARTZ (1800) was the first to distinguish "Orchider med en Anthera" and "Orchider med twå Anthera", more recently generally referred to as the *Monandrae* and the *Diandrae*. Apparently still under the spell of Linnaeus' views, and not realising that there is a difference between episepalous and epipetalous stamens (in other words that two whorls of stamens may be present), SWARTZ did not raise these groups to family level. This theory goes back to Robert BROWN, after he had studied *Apostasia* (see WALLICH: Plantae Asiaticae Rariores (1830), Vol. I, p. 74). BLUME, who described *Apostasia odorata* in 1825, had classified the species among the Orchids Subtrib. III. *Pulvereae*, B. *Diantherae* (p. 423). LINDLEY is the systematist who has enriched orchidology with his magnum opus *The Genera and Species of Orchidaceous Plants* (1830–1840). In the introduction on p. XVI (1840?) the author writes the following about *Apostasia*: "It may, however, be observed that Apostasia has apparently as much claim to be regarded as a diandrous monadelphous Amaryllidaceous plant allied to Hypoxidae . . . as it has to be regarded as a trilocular Orchidaceous plant with the gynandrous organization lost." LINDLEY had previously published (1833) his Nixus Plantarum where, on p. 22, he gives the following division:

Cohors II. GYNANDRAE

Monandrae	233. Orchideae
Diandrae, ovario 1-loculari	234. Cypripedieae m.
Diandrae, ovario 3-loculari	235. Apostasieae m.

He does not mention this booklet in the bibliography of orchids, published in his main work of 1840, but it does occur in 1853 in the third edition of his book: The vegetable Kingdom (p. 184) under the heading *Apostasiaceae*, (which are treated as a separate family there, immediately after the *Orchidaceae*). In 1833 Lindley regarded the *Gynandrae* as an order comprising three families, but in his principal work of 1840 he included the *Cypripedieae* again in the *Orchidaceae*.

I do not know the reason why he changed his mind, considering that Darwin and others later pointed out the great difference between the *Monandrae* and the *Diandrae*. In his book: *The various contrivances by which Orchids are fertilised by Insects*, he says about *Cypripedium* (p. 226): "(It) differs from all other Orchids far more than any other two of these do from one another. An enormous amount of extinction must have swept away a multitude of intermediate forms". DARWIN (1890), however, distinguished the *Cypripedeae* only as a tribe.

My personal view is that there are sufficient arguments to distinguish the *Cypripediaceae* as a family (and likewise the *Apostasiaceae*).

Lindley treats the latter as a separate family, in which he was followed by Ridley, Hutchinson, Godfery, Schlechter, Schweinfurt and Pulle, whereas others (Pfitzer, Smith, Holttum etc.) retain them as a tribe or subfamily of the *Orchidaceae*.

In the following pages I shall attempt to show that the order of the *Orchidales* ought to be considered to comprise three families:

1. *Apostasiaceae* Lindl. (*Apostasieae*)
2. *Cypripediaceae* Lindl. (*Cypripedieae*)
3. *Orchidaceae* s.s. de Juss. (*Orchideae*)

2. THE CHARACTERISTICS OF THE ORCHIDALES

The common characteristics of the Order of *Orchidales* are:

1. Herbaceous (rarely suffruticose), perennial plants with a sympodial, less often monopodial, growth, with only adventitious roots. As storage organs rhizomes, tubers, corms or pseudobulbs are present. Rarely hapaxanth (=monocarp, i.e., dying off after having flowered only once).

2. Leaves parallel- or curviveined, in the bud convolute (twisted) or duplicative (infolded from the mid-vein, the margins touching one another) leaves with or without an articulation between sheath and blade, the latter deciduous in the articulated type. Sometimes leaves squamiform in heterotrophic plants: *Orchidaceae* only.

3. Flowers in indeterminate inflorescences, which are terminal (acranth) or lateral (pleuranth); rarely flowers single; or, in the *Cypripediaceae*, inflorescence cymose.

4. Flowers zygomorphic, epigynous, hermaphrodite (rarely unisexual). The ovary has six connate parts, sometimes with a collar (calyculus) below the perianth. There are three placenta, on the three parts on which the petals are inserted. The median petal, forming the lip (labellum), differs in shape from the sepals and the two lateral petals.

5. The ovary topped inside the perianth by a column (gynostemium) supporting the androecium and the stigma; this column sometimes hardly developed (rarely missing), mostly distinct, short or more or less elongate.

6. Of the, in the fundamentally regular, trimerous monocotyledonoul flower diagram assumed double whorl of 3 stamens, only the abaxias ones ($A_1 + a_1 + a_2$) developed (fig. 1); rarely all three fertile (only in *Neuwiedia* Fig. 2), mostly only A_1 fertile (*Monandrae* Fig. 5.8), and sometimes $a_1 + a_2$ fertile (*Apostasia* and *Cypripediaceae* Fig. 3).

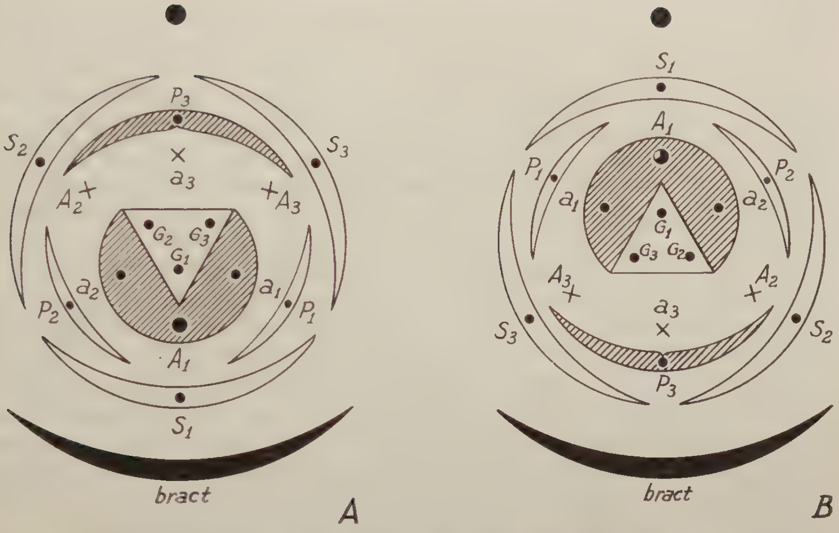


Fig. 1. Two diagrams of the flower of the *Orchidales*. A: not resupinated; B: resupinated. S_1, S_2, S_3: sepals; P_1, P_2: lateral petals; P_3: median petal or lip; A_1, A_2, A_3: stamens of the outer whorl of which A_1 is fertile or staminodial and A_2 and A_3 are always missing; a_1, a_2, a_3: stamens of the inner whorl of which a_1 and a_2 are fertile, staminodial or missing and a_3 is always missing; G_1, G_2, G_3: three vascular strands of the style of which G_2 and G_3 are sometimes missing. The gynostemium is formed by $A_1 + a_1 + a_2 + G_1 + G_2 + G_3$.

7. On the gynostemium the sessile stigma with three or two stigmatic lobes.

8. The flowers are entomophilous, sometimes ornithophilous, rarely autogamous.

9. Fruit a unilocular or trilocular capsule, opening with six fissures; sometimes baccate in *Neuwiedia*, *Galeola*.

10. Seeds minute, anatropous, very numerous, and with undifferentiated germ, the latter developing by mycotrophy (fungus symbiosis), into a protocorm with one growing-point. Radicle lacking.

Ad 1. In connection with the perennial habit, many orchids have storage organs; these are sometimes rhizomes, sometimes tubers (*Orchis*) or corms (*Gastrodia*). Especially in tropical species, pseudobulbs may occur, i.e., internodes, in which storage food is assembled (in the *Epidendranthae*). Most tropical species live on trees as epiphytes; studies made by Dr. Jacoba Ruinen (1952) have rather convincingly shown that the symbiontic fungus may be parasitic on the supporting tree.

Ad 2. Most orchids have convolute leaves in bud, only in the *Cypripediaceae* and the *Epidendranthae* (e.g. *Sarcochilus*) also duplicative leaves occur. Articulated leaves with deciduous blade are only found in *Epidendranthae.*

Ad 3. The inflorescence is indeterminate in the *Monandrae* and the flowers are always inserted in the axil of a bract. In some species the flower is terminal. An adossed bracteole is only found in *Cypripediaceae* (which sometimes have a centrifugal inflorescence). HAGERUP (1959) thinks that in the orchids the bracteolae are represented by sepals.

Ad 4. The strong trend towards zygomorphy and specialised insect pollination in this group has caused a considerable diversity of development of the perianth lobes. The labellum is small in *Platanthera* and *Disa,* but strongly developed in *Ophrys, Disperis* etc., it is of a relatively simple structure in *Brassavola* and *Cattleya*, but much more complicated in *Stanhopea* and *Coryanthes.* In other families of plants zygomorphy is often also associated with a diversity of development of the floral appendages. For instance, in several genera of the *Lamiales* (*Labiatiflorae*) as in *Anthirrinum*, *Lamium* etc. the lower or anticous lip of the corolla, though homologous with one petal, is bilobed.

In *Linaria* the lip is strongly differentiated ("masked"). Similar phenomena also occur in *Lobelia* and in quite a number of other genera. Among the Monocots, the *Zingiberaceae* possess a labellum, staminodial in origin and homologous with two connate stamens. This labellum lies inside within the petals.

In *Linaria* we find a small rudiment of the median, episepalous stamen inserted opposite and on the superior (posticous) lip. Nowhere, however, do we find an indication of parts of the perianth and the androecium merging into a single organ, which would, in addition, have required an inward or outward shift of either the one element or the other. The shape of the labellum is often particularly adapted to the pollination mechanism, as in *Ophrys*, *Pterostylis*, *Coryanthes*, *Cypripedium* etc. In *Satyrium*, whose flowers are not resupinated, the labellum has two spurs and at the entrance of each spur lies a viscid disc. In *Disa uniflora* the flower is resupinated, but the labellum is small and the median sepal has a spur lying behind the viscid discs of the stamen; this is another adaptation to a specific pollination mechanism. The genotype apparently determines the degree of zygomorphy, sometimes associated with a strongly developed lip, sometimes with a median sepal. This is of course concomitant with different forms of entomophily.

For the ovary, see 10.

Ad 5. There are different opinions concerning the nature of the gynostemium. Formerly it was believed to be a coalescence of the style and one or more stamens. Pfitzer defended the opinion that it is an apical extension of the receptacle. It could also be an apical extension of the coalesced parts constituting the ovary. A number of differentiations occurring in the column, such as the chin and the foot, can hardly be regarded as of stylar derivation. Sometimes, as in

Orchidoideae, the filament can not be distinguished from the column. Here apparently the filament forms a part of the column. In other cases, viz. in such *Epidendroideae* as *Cephalanthera*, *Epipactis* and *Epipogium*, a short filament is inserted on the column. In the *Apostasiaceae*, where the coalescence into a column is not very pronounced, stamen(s) and style can clearly be distinguished as separate, individual organs. In *Goodyera* and *Spiranthes* the column is also short, and style and stamen are connected by a thin lateral tissue. In particular species of the Australian genera *Diuris*, *Prasophyllum*, *Thelymitra*, etc., style and androecium are quite free and, accordingly, we can not speak of a proper gynostemium in these cases. Sometimes the column attains an appreciable length, as in the South African genus *Satyrium*, in some Australian genera such as *Caladenia*, and in many epiphytes such as *Cattleya*, *Cymbidium*, *Cycnoches*, etc. In connection with the development of the androecium, the gynostemium is always clearly zygomorphic and accordingly also the flower, even if the parts of the perianth sometimes differ very little among themselves, as in *Neuwiedia*, *Apostasia*, *Thelymitra*, etc., in whose flowers a whorl of three sepals alternating with a whorl of three petals can clearly be distinguished.

Ad 6. The reduction of the adaxial (axis-opposed) stamens ($A_2 + A_3 + a_3$) has left its mark on the development of the orchid flower.

A comparable case of unequal development of adaxial and abaxial stamens is provided by some *Commelinaceae* such as *Commelina*; in their non-resupinated flowers the adaxial stamens are fertile, the abaxial ones sterile. In the *Pontederiaceae* a progressive reduction can be observed, some genera having 6 stamens in two unequally developed groups of three, ($A_1 + a_1 + a_2$) being opposed to ($A_2 + A_3 + a_3$) (e.g., in *Eichhornea* and *Pontederia*), but the genus *Heteranthera* having only $A_1 + a_1 + a_2$ (a situation we also find in *Neuwiedia*) and the extreme case, *Hydrothrix* from Brazil, only A_1 (see GOEBEL, Flora **105**, 1913). In the *Philydraceae* only A_1 develops (see HAMANN, 1961). In the *Orchidales* only the abaxial stamens ($A_1 + a_1 + a_2$) are present, whereas the adaxial ones have completely disappeared. We often find only A_1. One should bear in mind that an extreme reduction of the number of stamens may also have occurred in forms that primarily underwent a reduction of one of the two whorls of stamens, as in the commelinaceous *Palisota* or in *Iridaceae*. If in *Iridaceae*, having only $A_1 + A_2 + A_3$, only the abaxial stamen A_1 would remain, a situation comparable to the one in the *Orchidoideae* would result. If in a plant of this group one or both of the normally absent stamens would atavistically develop, it is likely to be A_2 or A_3, or both of them, and not a_1 or a_2 as one would expect, because these two should be present in the form of the auriculae (see in this connection also 9).

Ad 7. The number of stigmatic lobes is three in the *Apostasiaceae* and *Cypripediaceae*. In *Apostasia* the stigmatic lobes are not very distinct. In the *Orchidaceae* s.s. (*Monandrae*) we can sometimes very clearly distinguish three lobes (*Disa*) but in other genera there are only two

(*Pterostylis*) which are also sometimes placed on stigmaphores (*Habenaria*). Upon closer examination, most *Monandrae* appear to have three stigmatic lobes and it is, threrefore, highly improbable that, as Darwin suggested, the median stigmatic lobe became the rostellum, but the rostellum sometimes forms a part of this stigmatic lobe, it is true, viz. in the *Epidendroideae*.

Ad 8. Many orchid flowers have structures eminently adapted to pollination by certain insects. This particularly holds true for flowers which are pollinated by pseudocopulation of male animals or for those which have a motile labellum. The investigations of the Australian worker Edith COLEMAN (1927) have been epoch-making. In Europe, the work of KULLENBERG (1961) has yielded excellent results. Flowers which are pollinated by humming birds are small and compact as in *Elleanthus* and *Isochilus*. The work of Stefan VOGEL (1959) provides, by inference, fine examples, of insect adaptations in South African species even if the actual pollination process has not been observed. In America, Dodson cooperates in this field with Van der Pijl, The Hague.

Ad 9. In *Neuwiedia singaporeana*, *N. javanica*, and *Galeola javanica* baccate fruits occur as in several *Commelinaceae*, but otherwise always capsules are found. *Neuwiedia*, *Apostasia*, *Paphiopedilum*, *Phragmopedium* and *Selenipedium* have trilocular capsules (also *Lecanorchis*?). In all other orchids unilocular capsules occur. The fruit is a so-called replum and opens with six longitudinal fissures, arising on either side of the six parts forming the ovary. The placentae, which are sometimes clearly branched, as in *Epipogium*, are connate with the three broad parts. The narrow parts, which at their top pass into the sepals, bear no placentae but form the stigmas.

Ad 10. The germination is in nature consistently associated with the presence of a fungus. After a few weeks the seeds form root hairs, when they are kept in moist surroundings, but the germination only proceeds after an infection with a symbiontic fungus (mostly *Rhizoctonia*) has taken place. An undifferentiated germ subsequently develops which is called the protocorm and possesses only one growing-point. The protocorms are often white and then for their nutrition depend entirely on the digestion of the fungus balls that have penetrated the root cortex (mycotrophy). It is often said that the seedlings live saprophytically, but this is incorrect; they live as parasites at the expense of their root fungus. The protocorms of many *Epidendroideae* soon turn green, and then become partly autotrophic.

N.B. It should be noticed that neither the presence of pollinia nor that of a rostellum have been mentioned as features of the order.

3. THE PLACE OF THE ORCHIDALES AMONG THE MONOCOTYLEDONS

In the various systems of classification the *Orchidales* or *Gynandrae* are consistently placed among the terminal orders of the Monocots and that is of course rather obvious, if they are regarded as the most evolved family, which, moreover, contains, in several of its subordinate taxa, genera which are still in speciation (*Orchis*, *Dactylorchis*, *Ophrys* etc.).

Von Wettstein places them after the *Scitamineae*, Takhtajan puts them after the *Haemodorales* in the 'super-order' of the *Liliiflorae*. Hutchinson removes the *Apostasiaceae* to the *Haemodorales* and associates them with *Curculigo* (*Hypoxidaceae*), whilst placing the *Orchidales* behind the *Burmanniaceae*. In the dendrogram proposed by HUTCHINSON (Vol. I, ed. 2, p. 694) the *Apostasiaceae* are considered to be the ancestors of both the *Burmanniaceae* and the *Orchidaceae*. In connection with the development of zygomorphy in the androecium it seems to me more obvious to suppose that the *Orchidales* are more closely related to the *Commelinales* than to the *Liliales*. Both the *Commelinales* (not the *Tradescantia* group) and the *Orchidales* show a tendency towards an unequal development of the adaxial stamens as opposed to the abaxial ones. This feature is, in my opinion, indicative of a close affinity of these two orders, so much so that they form a "natural" group. Considering that not infrequently (see, e.g., *Ophrys*, *Cymbidium*) the *Orchidales* exhibit clearly distinct whorls of sepals and petals (differing in both shape and colour), one could also include them in Hutchinson's *Calyciferae*.

Apart from the *Commelinaceae*, this group would, then, include the *Pontederiaceae*, of which HUTCHINSON says (Vol. I, ed. 2, p. 618): "the Pontederiaceae are a difficult family to place". The order *Commelinales* would then consist of the families *Commelinaceae*, *Pontederiaceae* and *Philydraceae*.

According to this classification, the *Orchidales* would then immediately follow this order. Particularly the *Pontederiaceae* are in some ways reminiscent of the *Apostasiaceae*. The genus *Heteranthera*, for instance, like *Neuwiedia*, has only the three abaxial stamens ($a_1 + A_1 + a_2$) developed, whereas the genus *Hydrothrix* possesses only one fertile stamen, A_1, like the *Monandrae*. In the *Commelinales* we usually find a well-developed endosperm, but it is lacking in the mycotrophic *Orchidales*. However, the *Commelinales* never possess a gynostemium.

4. THE CLASSIFICATION OF THE ORCHIDALES INTO FAMILIES

Although in 1833 LINDLEY suggested a subdivision of the *Gynandrae* into three families, he did not maintain this classification in his most important publication "The Genera and Species". He still treated the *Apostasiaceae* as a separate family, it is true, but the *Cypripediaceae* are included in the *Orchidaceae* as a tribe. If we consider what criteria are usually applied to delimit families, we must admit that it depends upon the group under consideration (and on the author!), but, generally speaking especially the inflorescences, the construction of the flower and particularly the androecial and gynoecial morphology (stamens and pistils) are taken into account. In the *Zingiberales*, for instance, we see that the reduction of the androecium plays an important part in the distinction of the *Musaceae* with three + two fertile stamens, the *Zingiberaceae* with one fertile stamen + staminodia, and the *Marantaceae* and *Cannaceae* with half a fertile stamen + staminodia, respectively.

In the *Liliales* the androecium also forms an important characteristic to distinguish various families. In the *Amaryllidaceae* (according to Eichler, 1875) we find 3 + 3 stamens, in the *Iridaceae* 3 + 0, in the *Haemodoraceae* 0 + 3. These are examples from the Monocots. Among the Dicots the recognised differences between the *Apocynaceae*, the *Periplocaceae* and the *Asclepiadaceae* provide and example. In the *Apocynaceae* there is no gynostemium and no corona, the anthers converge, the pollen grains are free, and the style ends in a stigmatic head; in the *Periplocaceae* there is a gynostemium and sometimes also a corona, the pollen grains are loose or the grains from one theca are so coherent that they are transferred as a whole, and the style has a stigmatic head; in the *Asclepiadaceae* a gynostemium, a corona, pollinia, translators and a stigmatic head are all present. These three families are markedly entomophilous. Similar differences occur in the three groups of the *Orchidales*, so that, in analogy of the examples mentioned, I propose to distinguish three families: *Apostasiaceae*, *Cypripediaceae* and *Orchidaceae* (sensu stricto).

Lindley was the first to treat the *Apostasiaceae* as a separate family and many taxonomists have followed him. Pfitzer united the *Apostasiinae* and the *Cypripedilinae*, first as *Diandrae* (1887), but later as *Pleonandrae* (1903), on account of the three or two fertile stamens. In the Orchid Review 40 (1932) p. 355, Colonel M. J. Godfery summed up the differences between the *Apostasiaceae* and the *Diandrae* (see also Charles Schweinfurth in Withner: The Orchids (1959), p. 511). Noteworthy is the statement by J. J. Smith in: Nova Guinea, vol. XII, botanique, livr. III, p. 175 under *Apostasia papuana* Schltr., (translated): "Ridley and Schlechter consider *Apostasia* and *Neuwiedia* to form a natural family, the *Apostasiaceae*. This is partly a matter of opinion; the delimitation of a family can be made more narrowly or more widely. However, if one accepts the *Apostasiaceae* as a family, the recognition of a family *Cypripediaceae* is certainly unavoidable." The differences between *Apostasiaceae* and *Cypripediaceae* are represented in the following table:

	Apostasiaceae	*Cypripediaceae*
Inflorescence	Flowers small in an indeterminate inflorescence	Flowers large, single or in a cymose inflorescence
Flowers	Uniformly yellow or white	Flowers multi-coloured
Perianth	Somewhat zygomorphic, the labellum slightly differing in shape from the other tepals	Strongly zygomorphic, lateral sepals connate, labellum slipper-shaped
Gynostemium	Very short, style and stamens (almost) completely free	More or less elongate, thick and curved; stamens with very short filaments

	Apostasiaceae	*Cypripediaceae*
Anthers	Large, oblong, versatile or basifixed and non-motile	Small, ovoid to globose, non-versatile
Pollen	Dry, powdery	Sticky (in *Phragmopedium* in pollinia)
A_1	In *Neuwiedia* fertile, in *Apostasia* tending towards reduction, thread-like or (in *Adactylus*) lacking	Developed as a large staminode at the base of the slipper and reducing its aperture to two small openings
Style	Erect, slender with three small terminal, stigmatic lobes	Thick and recurved into the slipper, with three large, terminal, stigmatic lobes
Resupination	By torsion	The ovary with a sharp bend at the apex

The mode of germination of the *Apostasiaceae* as yet still being unknown, it is not certain that the germ develops as a protocorm. Here, too, the seeds are minute, which suggests mycotrophy. In this family, the roots are hard and course, and thus different from the roots of the *Cypripediaceae*, which, though also thick, are fleshy and soft to the touch instead of woody as in the *Apostasiaceae*.

The differences between the *Cypripediaceae* and *Orchidaceae* s.s. correspond very well with those between the *Apocynaceae* and the *Asclepiadaceae*. The last two families have a clavate pistil, topped with 5 small stigmas. The *Apocynaceae* have loose pollen grains in the converging stamens; but connate stamens, a corona, pollen coherent in pollinia and translators are typical of the *Asclepiadaceae*. Both families are entomophilous, but the *Asclepiadaceae* are more specialized in that the pollinia and the translators play an important part in the process of pollination. In *Cypripediaceae* and *Orchidaceae* a gynostemium is present, but they have a differently developed androecium. The *Cypripediaceae* have sticky but loose pollen grains and no rostellum, the *Orchidaceae* pollinia, and a rostellum as an aid in transport of the pollen during insect pollination. These two families are also entomophilous. Their distinguishing characteristics are represented in the following table:

	Cypripediaceae	*Orchidaceae s.s.*
Inflorescence	Flowers with adossed bracteole, sometimes aggregated in the shape of a rhipidium, (flower sometimes solitary)	Flowers without bracteole, in racemes, spikes or panicles, (flower occasionally solitary)
Flower	Large; lateral sepals connate, labellum slipper-like	Different in size, lip rarely slipper-shaped
Gynostemium	Thick, recurved	Erect, sometimes with differentiations (foot, chin etc.)

	Cypripediaceae	*Orchidaceae s.s.*
Androecium	$\dagger A_1 + a_1 + a_2$; epipetalous stamens fertile, the episepalous one staminodial	$A_1 + \dagger a_1 + \dagger a_2$ or $A_1 + 0$; episepalous stamen fertile, the epipetalous ones staminodial or missing
Pollen	Sticky, in tetrads (only in *Phragmopedium* in pollinia)	In pollinia or in tetrads, sometimes rather loose, sometimes in massulae, occasionally waxy or cartilaginous
Rostellum	None	Present, sometimes strongly developed
Stigma	Terminal with three stigmatic lobes	Frontally directed towards the labellum, sometimes secondarily terminal; usually three-lobed, sometimes third lobe with rostellum or this lobe lacking

The *Apostasiaceae* include the Asiatic and Australian genera *Neuwiedia* and *Apostasia*. Forms resembling *Apostasia*, but without a staminodial A_1, are sometimes classified in a separate genus, *Adactylus*.

The *Apostasiaceae* occur in South and East Asia: India, from the Himalayas and Birma to Japan, throughout Indonesia and extending far into North Eastern Australia. The *Cypripediaceae* comprise four genera: *Cypripedium*, occurring in the temperate regions of Eurasia (extending far into the Himalayas) and in North America, *Paphiopedilum* from tropical Asia including Indonesia and extending to New Guinea, *Phragmopedium* found in America from Costa Rica extending into Bolivia and Brazil, and, finally, *Selenipedium*, also American and extending from Panama far into Brazil.

By far the greatest family is that of the *Orchidaceae* with hundreds of genera and thousands of species occurring all over the world, except in permanently snow-and ice-bound regions and in the deserts. This family shows an amazing variety in habit and in floral morphology. As one of the apparently most evolved families in the Monocots it is likely to be a relatively young group. In several genera the speciation is still in progress.

5. THE CHARACTERISTICS OF THE RESPECTIVE FAMILIES

Key to the families

1a. Flowers with at least two fertile stamens. Pollinia and rostellum absent. Stigma morphologically situated above the insertion of the stamens. Fruit trilocular or unilocular 2

b. Flowers with only one fertile stamen. Pollinia and rostellum present. Stigma on an erect column below and on the labellar side of the anther, but by resupination of the column (*Satyrium*) sometimes above it. Fruit a unilocular capsule. . . . *Orchidaceae*

2a. Flowers less than 3 cm in diameter with approximately regular perianth, uniformly white or yellow. Episepalous stamen fertile or only represented by a thread-like staminode, sometimes entirely lacking. The epipetalous stamens with oblong anthers containing powdery pollen. Style with three small stigmatic lobes. Fruit a trilocular capsule or baccate. . . . . *Apostasiaceae*

b. Flowers more than 3 cm in diameter, manifestly zygomorphic with the median petal developed as a "slipper", never uniformly coloured. Episepalous stamen sterile, peltate, protruding from the base of the slipper. The epipetalous stamens with subglobose anthers containing sticky pollen. Style short and thick, recurved into the slipper, with three large stigmatic lobes. Fruit a unilocular or trilocular capsule . . . . *Cypripediaceae*

Description:

Fam. *Apostasiaceae* Lindl (Plate I, Figs. 2A and 2B). Terrestrial herbs with a subterraneous rootstock bearing hard adventitious roots. Stem sympodial, with scattered pleated leaves. Inflorescence a simple or ramified terminal raceme. Flowers white or yellow, resupinate by torsion of the pedicel. Perianth scarcely zygomorphic (median petal of approximately the same shape as the other parts). Gynostemium short to very short (not formed by the receptacle), without pollen bed. The episepalous stamen fertile, staminodial or missing. The epipetalous lateral stamens fertile; anthers versatile on filaments or basifixed, erect, always longer than broad, with powdery pollen (no pollinia). No rostellum. Style thin, straight or recurved, with three or two small apical stigmatic lobes, style exceeding or equalling the tops of the anthers, its lobes usually exceeding them. Ovary when ripe with three chambers forming a trilocular capsule or a leathery berry. (See however Plate IV, Fig. 9). Seeds small with sometimes membranaceous testa. Germination not known.

Fam. *Cypripediaceae* Lindl. (Plate I, Figs. 3A and 3B). Terrestrial herbs with short rootstock bearing thick and fleshy adventitious roots. Stem sympodial with scattered leaves along the stem, or leaves densely crowded at the base, convolutive or duplicate. Inflorescence terminal, cymose, with 1-many flowers. Flowers never uniform in colour, resupinate by a sharp bend in the top of the ovary. Perianth zygomorphic; the lateral sepals usually concrescent, situated below the slipper-shaped lip which represents the median petal. Gynostemium thick and recurved into the slipper (with participation of the receptacle?); no pollenbed. Episepalous stamen represented by a more or less peltate staminodium at the base of and partly exerted from the slipper, so that two narrow openings form the exits from the slipper; epipetalous stamens fertile, with short filaments, anthers subglobose, with sticky pollen (no pollinia except in *Phragmopedium*). No rostellum, style short and thick, stigma apical with three large lobes inside the slipper above the fertile stamens. Ovary with one or three chambers forming a uni- or trilocular capsule. Seeds small with membranaceous testa. Protocorm white and mycotrophic.

Fam. *Orchidaceae* Lindl. (Plate II, Figs. 4A, 4B, 5A, 5B, Plate III, 6, 7, 8A, 8B). Terrestrial or epiphytic herbs, with a rootstock or tubers and a number of thick or thin adventitious roots. Stem monopodial or sympodial, with scattered duplicated or convolute leaves or leaves reduced to scales, sometimes the lower internodia forming pseudobulbs. Inflorescence terminal (acranth) or lateral (pleuranth), racemose, a panicle, raceme or spike (rarely a capitulum, an umbel or a spadix), with few to many flowers of various colours. Flowers nearly always resupinate by torsion or by a bend near the top of the ovary (*Ophrys*). Perianth zygomorphic, the median petal forming a lip (only exceptionally slipper-shaped) and sometimes spurred. Gynostemium of various shapes, sometimes formed with the participation of the receptacle and with differentiations (foot, etc.), short or long (rarely gynostemium lacking: *Thelymitra*, *Diuris*, *Prasophyllum*) straight or curved, sometimes with apical clinandrium (pollen bed). Episepalous stamen fertile (except in unisexual flowers); anther of various shapes, with or without filament, erect or declined over the clinandrium; the pollen always present in the form of pollinia. Epipetalous stamens missing or staminodial (sometimes represented by wings at the sides of the gynostemium); rostellum present (rarely lacking: *Cephalanthera*, *Caladenia*), provided with one or two, sometimes stipitate, retinacula. Style forming a part of the gynostemium, (rarely free: *Goodyera*, *Diuris* (Plate II, Figs. 4A and 4B), *Prasophyllum*) with three or two stigmatic lobes (the latter sometimes with two stigmaphores). Stigma, if the gynostemium is straight on the labellar side, frontal below the anther, in the alternative case, with curved gynostemium (*Satyrium* and allies), apical above the anther. Ovary with one chamber, forming a unilocular fruit (usually a replum). Seeds small with membranaceous testa (very rarely not membranaceous: *Vanilla*). Protocorm white or green, mycotrophic.

6. THE SUBDIVISION OF THE ORCHIDACEAE BY DIFFERENT AUTHORS

There is a remarkable difference in the proposed subdivision of the *Orchidaceae* between the Anglo-Saxon and the German groups of authors. Lindley, in his principal work, divided the family into seven tribes (*Apostasiaceae* being treated as a separate family), which tribes he treated as groups of equal rank. Bentham reduced this number to four, likewise equivalent groups. The American author Garay places the five groups which he distinguishes also in juxtaposition as subfamilies of which the *Apostasioideae* and the *Cypripedioideae* are two, apart from the *Neottioideae*, the *Ophrydoideae* and the *Kerosphaeroideae*. Dressler & Dodson approach the German viewpoint in so far that they distinguish two subfamilies, viz. the *Cypripedioideae* with the tribes *Apostasieae* and *Cypripedieae*, and the *Orchidoideae* with the tribes *Neottieae*, *Orchideae* and *Epidendreae*. As opposed to these systems, the Germans prefer a typically hierarchic system. Apart from the *Cypripedieae* and *Apostasieae*, Reichenbach fil. distinguished the *Ophrydeae* and *Operculatae*, of which the latter are subsequently divided into *Neottiaceae* and *Euoperculatae*, and the latter again subdivided into the *Arethuseae*, *Vandeae*, *Epidendreae* and *Malaxideae*. Pfitzer also proposed a typically hierarchic system, mainly based on vegetative characteristics. He divided the *Monandrae* into the *Basitonae* as opposed to the *Acrotonae* and the latter were again hierarchically subdivided as follows:

Acrotonae, pollinia apically connected with the rostellum

a. *Acranthae* (inflorescence terminal)

1. Convolutae (with convolute leaves)
   Continentes (lamina not deciduous)
   Neottiinae
   Articulatae (lamina deciduous)

2. Duplicatae (with conduplicate leaves)

b. *Pleuranthae* (inflorescence lateral)

1. Convolutae (with convolute leaves)
   Homoblastae (with thin stem or the stem thickened in a series of internodes.)
   Heteroblastae (with a single internode transformed into a pseudobulb)

2. Duplicatae (with conduplicate leaves)
   Sympodiales (with sympodial growth)
   Monopodiales (with uninterrupted, i.e. monopodial growth)

SCHLECHTER's system, now must current, owing to his well-known publication "Die Orchideen" (1915) corresponds rather closely with that of PFITZER. Unlike Pfitzer, Schlechter distinguishes the *Apostasiaceae* as a separate family and divides the *Orchidaceae* into two subfamilies: the *Diandrae* (comprising the *Cypripedilinae*) and the *Monandrae* (subdivided into the *Basitonae* and the *Acrotonae*). The *Acrotonae* are subsequently subdivided into the subdivision 1. *Polychondriae* (having pollen grains lying in tetrads inside the pollinia) and the subdivision 2. *Kerosphaereae* (with waxy or cartilaginous pollinia). Schlechter classifies the *Kerosphaereae* as follows:

Kerosphaereae Reihe A. Acranthae
Reihe B. Pleuranthae
Unterreihe I. Sympodiales
Unterreihe II Monopodiales.

In my opinion preference should be given to a hierarchic system, because it emphasises the assumed greater or smaller mutual affinity so much better. The recognition of three families not linked by transitions is inevitable if one strives for the conceivable most natural system of classification. In the *Orchidaceae* s.s., two clear-cut groups can be distinguished by differences in the structure of the gynostemium and the rostellum, without intermediate (transitional) forms, viz. the two subfamilies *Orchidoideae* and *Epidendroideae*. In the latter group, the contribe of the *Neottianthae* is opposed to the contribe of the *Epidendranthae* in which the anther is not very persistent and the pollen forms solid pollinia. This system corresponds in broad outlines with that of Reichenbach.

7. THE SUBDIVISION OF THE ORCHIDACEAE

In contradistinction to the small and rather uniform families *Apostasiaceae* and *Cypripediaceae*, the *Orchidaceae* excel in an overwhelming polymorphy. The considerable morphological diversity of this group requires a convenient subdivision. In my opinion two subfamilies ought to be distinguished, viz. the *Orchidoideae* (Dressl. & Dods.) Vermln. (=*Ophrydoideae* Garey=*Basitonae* Pfitz.) and the *Epidendroideae* Vermln. nov. subfam. (=*Operculatae* Rchb. fil. (1868) =*Acrotonae* Pfitz.).

The *Orchidoideae* have a broadly inserted stamen, invariably with two pollinia composed of massulae (pollen clumps), and with basitonic caudicles (i.e. their attachment is basitonic in respect of the rostellum). In this group, the rostellum is in principle a strip of tissue, a sometimes very massive tape, with a viscid disc on either side, and in its centre provided with an extension of the vascular bundle running in the median stigmatic lobe. (This is, to my mind, suggestive of the de novo formation of vascular strands in various places where a good translocation of solutes is required). The rostellum exhibits two diverging trends, the one being a progressive infolding of the "tape" which causes the retinacula to approach one another, and the other a tendency towards an appreciable increase in size with long extensions bearing the retinacula at their extreme ends (see VERMEULEN, 1965, p. 237) In the latter case the connective of the anther is often very broad. The rostellum, with in principle always two retinacula, is very characteristic of this subfamily. The basitony is equally characteristic: the pollinia are always basitonically attached to the retinacula of the rostellum by means of the two caudicles.

In *Cephalanthera* and in some Australian representatives of the *Neottieae* the pollinia are also attached near their base to the pollinator by means of viscid matter or a subbasal viscid disc, but in these forms the rostellum is missing or consists of a single and much more simple structure, and, moreover, the attachment is achieved without the intervention of caudicles.

The species of the *Orchidoideae* usually have tubers, much more rarely rhizomes, but never corms or pseudobulbs. The protocorm is white. They exhibit sympodial growth and occur mainly in the temperate regions of the northern and southern hemispheres, but do not constitute an important element in the floras of Australia and South America.

The genus *Habenaria*, recognisable by two stigmatic lobes inserted on stigmaphores, and allied forms are wide-spread throughout the tropical regions of the Old and the New World with a few species extending to Australia. The main massing centres of the *Orchidoideae* lie in temperate Eurasia, in North America and in South Africa.

The second subfamily, the *Epidendroideae*, comprises all genera not referable to the *Orchidoideae;* in this respect I follow Reichenbach fil. who distinguished this group as early as 1868 under the name of *Operculatae*. Pfitzer dubbed this group the "*Acrotonae*". In many genera belonging to this subfamily the more or less hollow top of the column forms a pollenbed (clinandrium or androclinium), the anther suspended above it, when ripe, deposing its pollinia into this pollenbed. Such a clinandrium never occurs in the *Orchidoideae*. In the majority of the *Epidendroideae* the anther is inserted on a short filament or it is attached only by one point and thus often falls off when the pollinia are removed. A broadly inserted anther occurs much more rarely in this group (*Hammarbya*). Although the number of pollinia usually corresponds with the number of loculi, so that there are four, occasionally there are eight, whereas in other cases two of the pollinia are reduced and the remaining two are solitary. Caudicles are not always present and if so, they stretch as far as the top of the pollinia where they are attached, in other words, they are acrotonic. Even if there are no caudicles, the viscid matter or the viscid disc lies on top of the pollinia. In the Eurasian genus *Cephalanthera* the pollinia are carried away by visiting insects, the viscid liquid of the stigma secreted in the proximity of the bases of the pollinia acting as an adhesive.

In several Australian genera (*Acianthus*, *Caladenia*, *Lyperanthus*) the pollinia likewise stick to the pollinator with the aid of an adhesive substance secreted near their base. One could speak of mesotony (sometimes even of basitony) in this case. The sticky matter or the viscid disc consists of a single mass or a solitary body, as a rule, which is excreted at the apex of the median stigmatic lobe, i.e., at its distal end. The viscid disc rarely replaces the lobe entirely as in *Pterostylis*. In the exceptional case of a bilobed or bifid rostellum, there is always a short and broad portion connecting the lobes (in contradistinction to the *Orchidoideae*), the rostellum being fundamentally solitary in this group, even if differentiations do occur. The vegetative development is rather varied in the *Epidendroideae*. This will be discussed under 8. The subfamily is chiefly represented in the tropics but extends to the cold regions.

Key to the subfamilies

1. Stamen broadly inserted, with two (double) pollinia, each at the base with a caudicle basitonically connected with the retinacula (viscidia) of the rostellum (rarely the two retinacula concrescent); pollen sectile (in massulae). Stigma with three or two lobes, in the last case lobes sometimes inserted on stigmaphores . . . *Orchidoideae*
2. Stamen with filament or basifixed (rarely broadly inserted) with 2–8 pollinia, sometimes with caudicles connected mesotonically

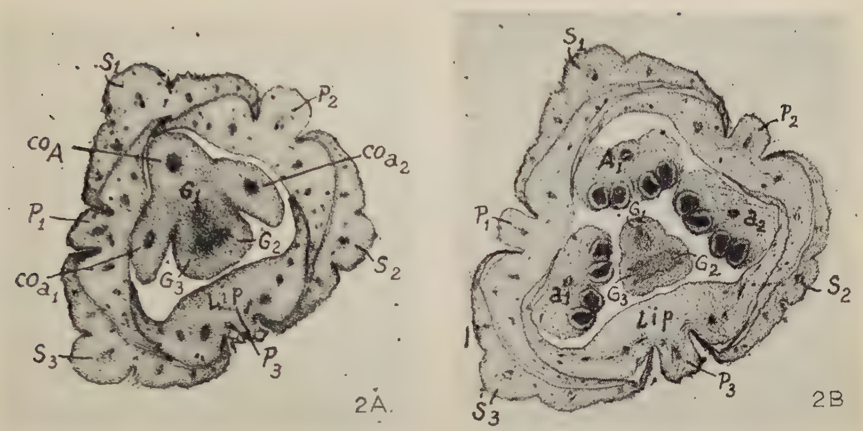
or acrotonically with the viscid matter or the viscidium (rarely split in two); pollen rarely sectile (in massulae). Stigma with three or two lobes never on stigmaphores . . . *Epidendroideae*.

1. Subfam. *Orchidoideae* (Dressl. & Dods.) Vermln. = *Basitonae* Pfitzer = *Ophrydoideae* Garey (Plate III, Figs. 8A and 8B). Gynostemium never with a pollenbed (androclinium) and anther never opercular. Stamen broadly inserted, usually on each side with an auricle. Anther with two (double) pollinia, each with a caudicle at the base and these caudicles connected with the basal rostellum (basitonic), anther sometimes with broad connective (so that the two thecae are found on the opposite sides of the stigma, as in *Satyrium* and *Disperis* and never deciduous. Pollen always in massulae. No staminodia. Rostellum forming a tape (*Coeloglossum*) or a voluminous body (*Bonatea*), with at each end a viscid disc (retinaculum), sometimes in a bursicula (*Ophrys*, *Orchis*), only in exceptional cases the two retinacula connate into one (*Anacamptis*, *Herschelia*, *Monadenia*). Retinacula always at the base of the pollinia at the caudicular ends, orbicular or oval, rarely oblong. Stipe always lacking. Stigma with three or two lobes, usually frontal (at the labial side) of the gynostemium, sometimes apical if the anther is reflexed (*Disa*, etc.) (If two stigmatic lobes are present sometimes each at the end of a stigmaphore and then always in the neighbourhood of a retinaculum which is found at the end of a thecal tube and rostellum arm, *Habenaria*).

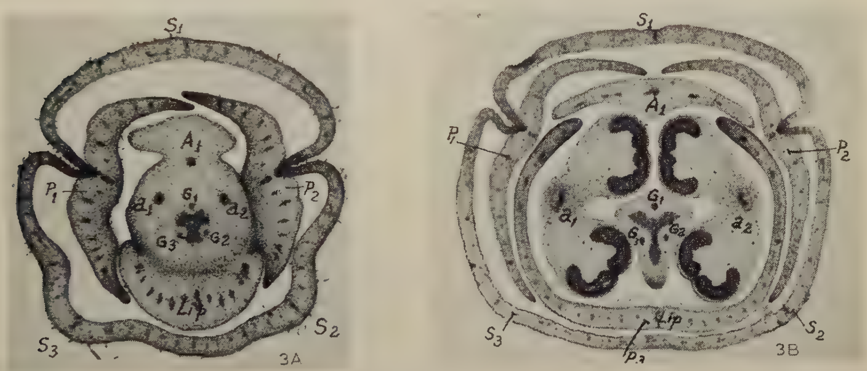
Terrestrial herbs, rarely more than 1 m high, growing sympodially with rootstocks or usually tubers. Stem with convolute inarticulated leaves, usually scattered, rarely opposite. Plants always with chlorophyll. Inflorescence always terminal, spicate or racemose. Flowers from 1–10 cm in diameter. Protocorm white.

2. Subfam. *Epidendroideae* Vermln. nov. subf. (= *Operculatae* Rchb. f. (1868) = *Acrotonae* Pfitz.)

Gynostemium often with an androclinium and anther opercular. Stamen with a short filament or sessile and basifixed (rarely broadly inserted: *Malaxis*), sometimes with an auricle on each side. Anther with two or more pollinia, sometimes with caudicles but these connected at the top of the pollinia, with the rostellum (acrotonic), anther only exceptionally with a broad connective (*Hammarbya*) and in many genera deciduous. Pollen grains in tetrads, rarely loose, or pollen waxy or cartilaginous and strongly coherent, rarely (*Epipogium*, *Stereosandra*) in massulae. Staminodes (a_1, a_2) sometimes represented by wings (*Diuris*, *Prasophyllum*) or only by vascular strands in the gynostemium, or missing. Rostellum forming a single organ at the apex of the median stigmatic lobe or replacing this lobe (*Pterostylis*) forming viscid matter (*Listera*) or a viscid disc, sometimes secundarily bifid (*Angraecum*, p.p.) Retinaculum acrotonic or mesotonic (in *Stereosandra* a part of the anther (Plate V; Figs. 13A, 13B; Plate VI, Fig. 14), none in *Cephalanthera*. In several genera a stipe, i.e., a part of the gynostemium forming the connection between rostellum and

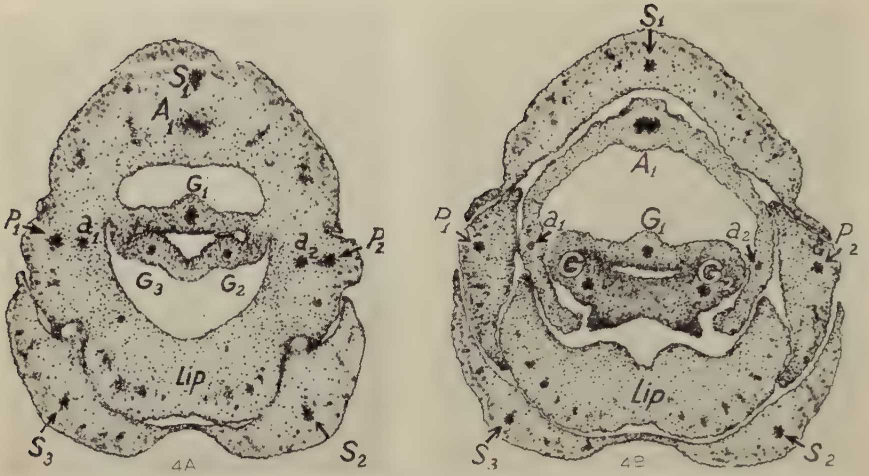


Figs. 2A and 2B. *Neuwiedia veratrifolia* Bl., two cross sections through a young flower bud; A: lower one with gynostemium (co_A vascular strand of stamen A_1; co_{a1} and co_{a2} vascular strands of the stamens a_1 and a_2 of the inner whorl. B: more distally cut section with the three anthers, each with four loculi, and the style with three vascular bundles.

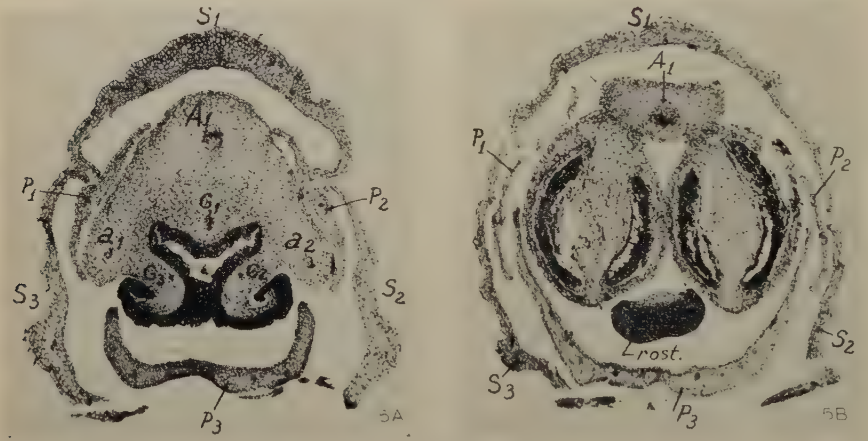


Figs. 3A and 3B. *Phragmopedium schlimii* Rolfe, two cross sections through a flower bud. A: lower one with the lip, A_1, a_1 and a_2 still connected with the gynostemium. B: more distally cut section with lip and staminodium A_1 free. The two stamens of the inner whorl (a_1 and a_2) each with four loculi.

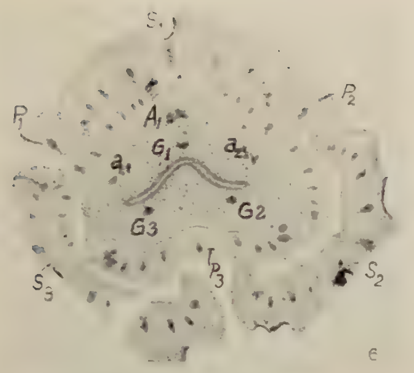
S_1: median sepal; S_2 and S_3: lateral sepals; P_1 and P_2: lateral petals; P_3: median petal or lip; A_1: vascular strand of the median stamen of the other whorl; a_1 and a_2: lateral stamens of the inner whorl; G_1, G_2 and G_3: vascular strands of the style.



Figs. 4A and 4B. *Diuris semilunulata* Messmer, two cross sections through a flower bud; A: lower one with a_1 and a_2 split off from P_1 and P_2. In B: the three stamens A_1, a_1 and a_2 still form a whole and G_1, G_2 and G_3 run in the style which is free so that a gynostemium is not realised. a_1 and a_2 become free higher up to form two wings.



Figs. 5A and 5B. *Limodorum abortivum* Sw., two cross sections through a young flower bud; A: lower one with three stigmatic lobes each with a vascular strand (G_1, G_2 and G_3) and a_1 and a_2 in the margins of the gynostemium. B: more distal one with A_1 with two thecae and each with two loculi.



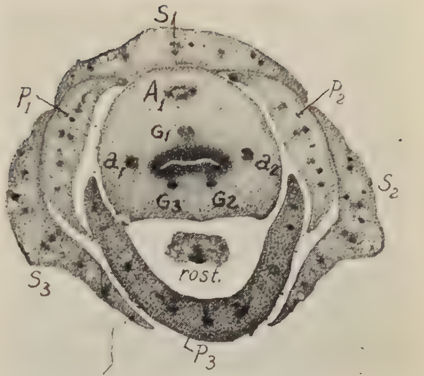
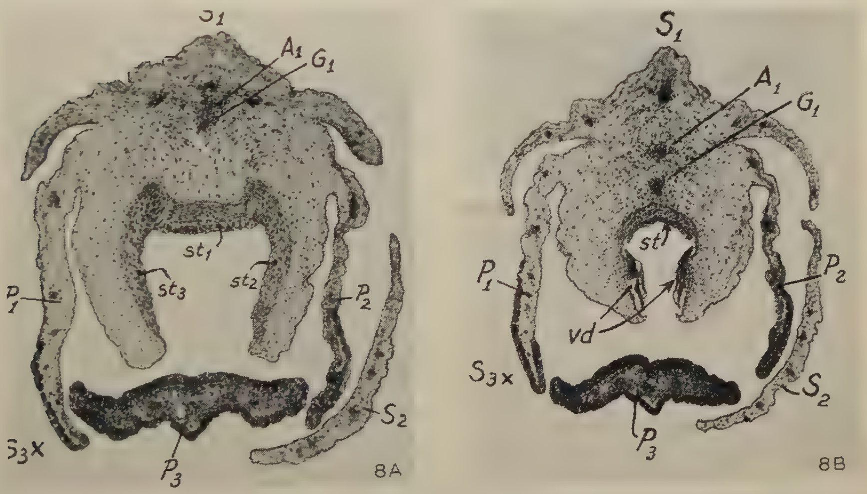


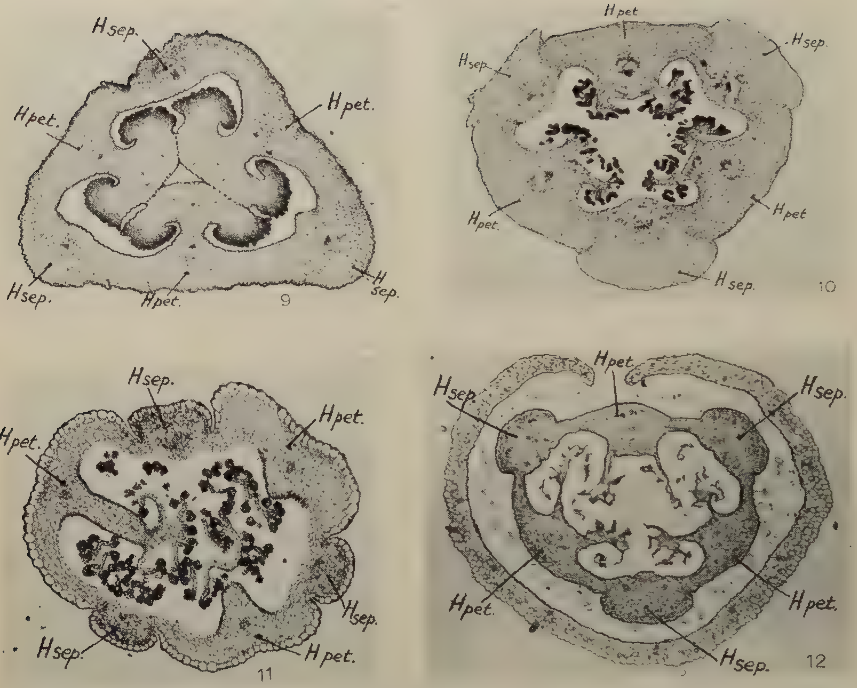
Fig. 6. Cross section through a flower bud of *Vanilla planifolia* Andr., also with vascular strands of A_1, a_1 and a_2.

Fig. 7. Cross section through a flower of *Aerangis coriacea* Summerh.



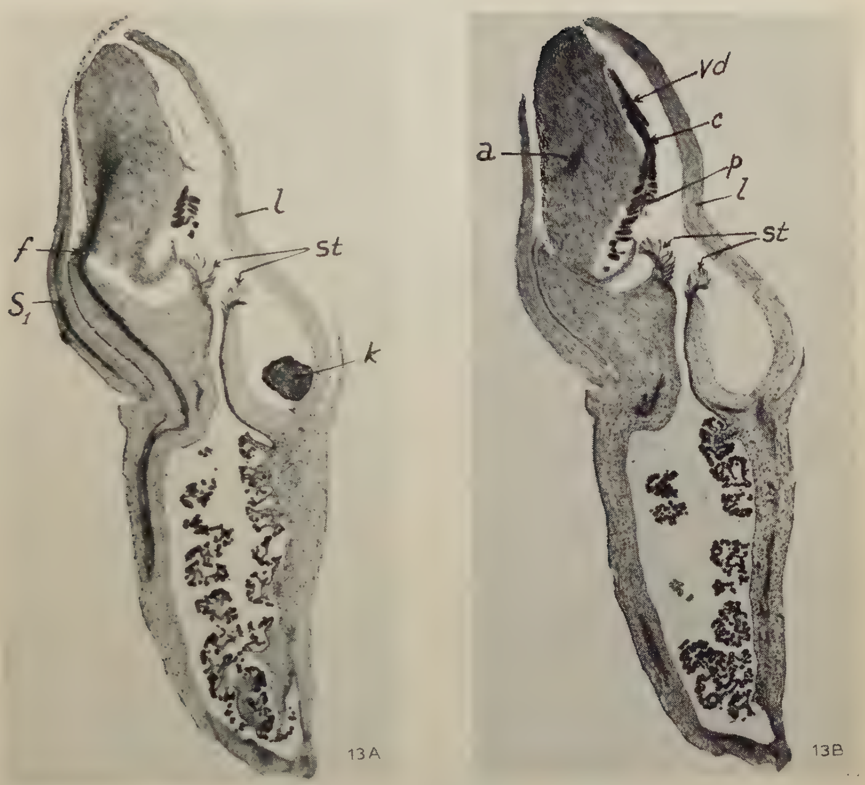
Figs. 8A and 8B. *Platanthera bifolia* (L.) Rich., two cross sections through a young flower bud; A: lower one with three stigmatic lobes (st_1, st_2 and st_3) and with the vascular strands of the stamen A_1 and the only one of the style still connected; B: more distally cut section with two viscid discs above the two lateral stigmatic lobes; A_1 and G_1 are now separated; only one vascular strand runs into the style.

Plate III



Figs. 9, 10, 11 and 12. Cross sections through the ovary of the flowers of four different species of orchids. Fig. 9 *Neuwiedia veratrifolia* Blume; Fig. 10 *Disa uniflora* Berg.; Fig. 11 *Schizodium inflexum* Lindl.; Fig. 12 *Caladenia* spec. H_{sep}: hyposepalous part of the ovarium; H_{pet}: hypopetalous part of the ovarium. In the centre of the figures the placentae are seen with the numerous ovules.

Plate IV



Figs. 13 and 13B. *Stereosandra javanica* Blume, two longitudinal sections through a young flower bud; S_1: median sepal; f: filament of the anther A_1; l: lip; st: two stigmatic lobes at the top of the style canal; K: gland on the lip. B is a section made near the middle of the anther a; vd: viscidium as part of the anther; c: caudicle; p: pollinium; l: lip and st: stigmatic lobes.

Plate V

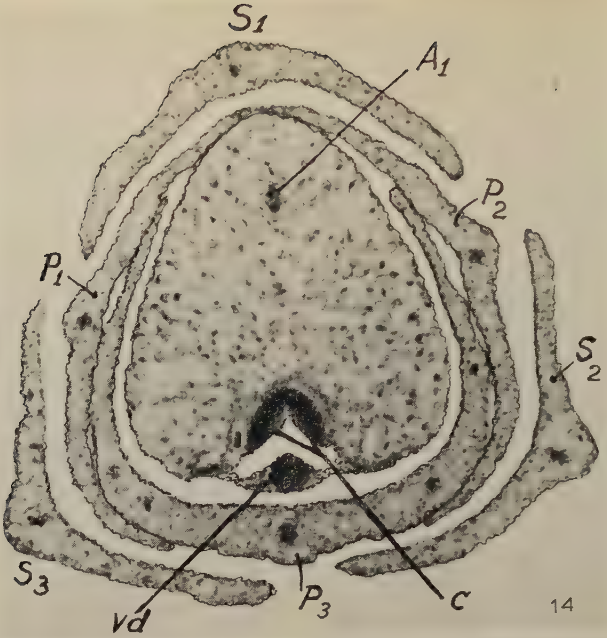


Fig. 14. Cross section through a young flower bud of *Stereosandra* Blume; A_1 is the vascular cord of the fertile stamen of the outer whorl c: caudicle, composed of two parts; vd: viscidium as part of the anther.

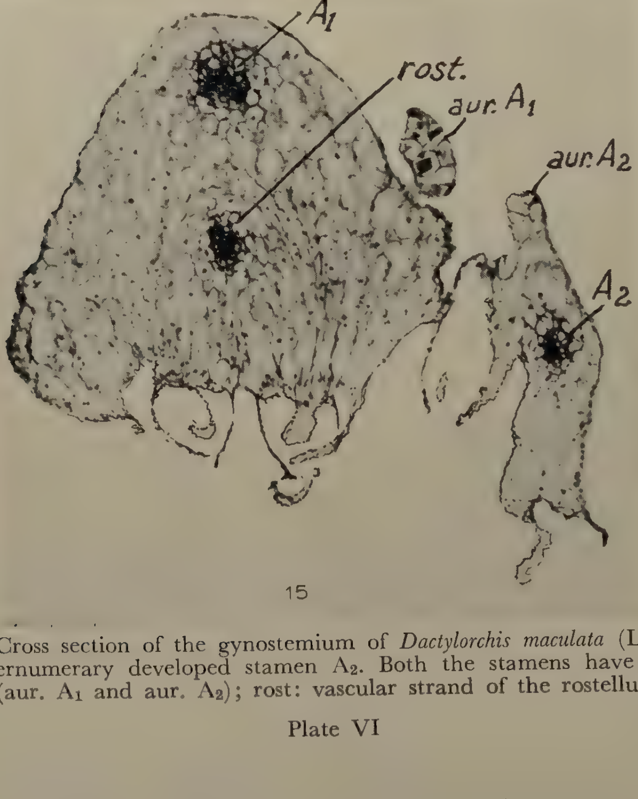


Fig. 15. Cross section of the gynostemium of *Dactylorchis maculata* (L.) Vermln. with supernumerary developed stamen A_2. Both the stamens have an auricle (aur. A_1 and aur. A_2); rost: vascular strand of the rostellum.

Plate VI

pollinia. Stigma with three or two lobes, frontal (at the labial side) of the gynostemium, its lobes never on stigmaphores.

Terrestrial herbs (rarely suffruticose), or epiphytes, varying from very small to several meters high, growing sympodially or monopodially, with rootstocks, tubers, corms or pseudobulbs, in monopods without storage organ (*Vanda*). Stem with convolute or duplicate articulated or inarticulated leaves, scattered or rarely opposite. Several genera without chlorophyll and if so, with reduced leaves. Inflorescence terminal (acranth) or lateral (pleuranth), a panicle, a raceme, a spike or rarely a spadix (*Megaclinium*), an umbel or a capitulum (*Cirrhopetalum*). Flowers varying from very small (*Taeniophyllum*) to 20 cm in diameter.

8. EPIDENDROIDEAE

In contrast to the *Orchidoideae*, the *Epidendroideae* do not form a homogeneous group, as may be concluded from the diagnosis. Two subordinate groups can be distinguished, which I have indicated as two contribes, viz. the *Neottianthae* and the *Epidendranthae*, a distinction made as early as 1868 by Reichenbach fil. who classified the *Neottianthae* as *Neottiaceae* and the *Epidendranthae* under *Euoperculatae*; it should be noted, however, that he also included the *Arethuseae* in the latter group, but I think that most of them are referable to the *Neottianthae*. The *Neottianthae* are mostly small terrestrial orchids, as a rule occurring outside the tropics, whereas the *Epidendranthae* are very often epiphytes with a mainly tropical distribution. Among the *Neottianthae* many forms occur which are practically devoid of chlorophyll and live as parasites on their root fungus (commonly referred to as "saprophytes"). In connection with their epiphytic way of life, it is among the *Epidendranthae* that we find forms with "pseudobulbs", aerial storage organs developing from one or more stem internodes, often containing photosynthetic tissue, rather well-known especially in our cultivated orchids. The pollen grains of the *Neottianthae* occur in tetrads, but sometimes they are quite free, only rarely arranged in massulae as in *Epipogium* and *Stereosandra* (Plate V, Figs. 13A and 13B). In *Acianthus* the pollen is sometimes waxy or cartilaginous, always tightly coherent into a solid mass.

The genera *Sobralia* and *Bletilla* (and some related genera) have granular pollen, but on account of their general habit they are classified among the *Epidendranthae*. Briefly summarized the differences are as follows:

> Contribe *Neottianthae*. Pollen grains in tetrads in two double pollinia, anther straight or opercular, rostellum never stipitate. Pseudobulbs never developed, plants often with rhizomes, tubers or corms. Inflorescence terminal (in *Vanilla* and allied forms lateral). Leafblades never early deciduous. Leaves in bud always convolute. Mode of growth sympodial (in *Vanilla* and some allied forms monopodial). Many genera lacking chlorophyll. N.B. *Sobralia*, *Bletilla* and their near-allies do not belong here.

Contribe *Epidendranthae*: Pollen waxy or cartilaginous, in two to eight pollinia, anther opercular, rostellum sometimes stipitate (sometimes the viscidium split in two and each half with an individual stipe). Pseudobulbs often developed, plants sometimes with rhizomes, never with tubers. Inflorescence terminal or lateral. Leaf blades sometimes early deciduous. Leaves in bud convolute or conduplicate. Mode of growth monopodial or sympodial. Plants with green trophophylls, rarely without leaves (*Taeniophyllum*; in the aphyllous epiphytic species belonging to this genus, the assimilatory function is performed by the exposed roots).

Contribus *Neottianthae*: Polline in turmis quaternis in duobus polliniis bipartitis; anthera erecta vel operculata, rostello non stipitato; nunquam pseudobulbis, saepe rhizomatibus vel tuberibus vel rhizocormis. Inflorescentia terminali (in Vanillinis laterali). Laminis non decidentibus. Foliis in gemma semper convolutis. Structura sympodiali (in Vanillinis monopodiali). Multa genera non virentia.

N.B. *Sobraliinae* et *Bletillinae* non huius contribus sunt.

Contribus *Epidendranthae*: Polline cerae vel cartilagini simili in 2—8 polliniis; anthera operculata; rostello interdum stipitato (nonnunquam viscidio bifido, utraque parte stipitata). Saepe pseudobulbis, interdum rhizomatibus, nunquam tuberibus. Inflorescentia terminali vel laterali. Laminis interdum decidentibus. Foliis in gemma convolutis vel complicatis. Structura monopodiali vel sympodiali. Herbae virentes.

The descriptions of the two contribes are as follows:

Contribe *Neottianthae* (Plate II, Figs. 4A, 4B, 5A, 5B; Plate III, Fig. 6): Gynostemium with straight or opercular anther and in the latter case provided with an androclinium. Sometimes gynostemium not developed, because anther and style are not concrescent (*Diuris*, *Prasophyllum elatum*, *Thelymitra rosea*). Stamen usually with an auricle on each side (*Goodyera*, *Epipactis*). Anther either straight and persisting or opercular and often deciduous, never with more than two double pollinia, sometimes with caudiculae (*Epipogium*, *Stereosandra*). Pollen in tetrads rarely loosely granular or waxy (*Acianthus*) or in massulae (*Epipogium*, *Stereosandra*). Staminodia ($a_1 + a_2$) sometimes developed as discrete wings (*Diuris*, *Prasophyllum*) or only represented by vascular cords in the margins of the gynostemium. Rostellum producing viscid matter or a viscid disc. Retinaculum acrotonic or mesotonic (in *Stereosandra* a derivative of the anther, in *Cephalanthera* missing). Stigma with three or two lobes (two in *Pterostylis*).

Terrestrial herbs or vines, green or white to brownish, sympodial (in *Vanilla* and related forms sometimes monopodial) with rootstock, tuber or corm but never with pseudobulbs. Stem with convolute leaves (or with sheaths only), inarticulate. Inflorescence terminal (in *Vanilla* and its near-allies pleuranth). Flowers varying from small to 10 cm in diameter, usually in a spike or raceme. Protocorm white.

Contribe *Epidendranthae* (Plate III, Fig. 7.). Gynostemium with a usually deciduous and operculate anther and an androclinium. Stamen rarely auriculate. Anther with 2–8 pollinia (sometimes with caudiculae: *Epidendrum*). Pollen waxy or cartilaginous. Staminodia ($a_1 + a_2$) sometimes represented by vascular strands in the gynostemium (*Aerides, Cattleya*), rarely developed as appendices (*Bulbophyllum*). Rostellum formed by viscid matter or a viscid disc, sometimes split. Retinaculum acrotonic. Stigma usually three-lobed.

Mostly epiphytic, less often terrestrial herbs, rarely suffruticose, green, sympodial or monopodial (*Vanda*), never with tubers but with rootstocks or with corms; pseudobulbs often occurring. Stem with convolute or conduplicate, sometimes articulate, leaves. Inflorescence terminal or pleuranth. Flowers varying from very small (*Taeniophyllum*) to 20 cm in diameter, in a panicle (*Oncidium*), a raceme or spike, rarely a spadix (*Megaclinium*), an umbel or a capitulum (*Cirrhopetalum*), Protocorm white or green.

Upon closer examination the two contribes appear to contain several natural groups, here treated as tribes. The most obvious ones are the three tribes of the *Neottianthae*: the *Neottieae, Arethuseae* and *Vanilleae*, the *Neottieae* being characterised by the erect stamen without a clinandrium (androclinium, pollen pouch), the *Arethuseae* by the presence of a pollen pouch, and the *Vanilleae* by their climbing habit (they are lianas) and their aberrant mode of growth.

The *Epidendranthae* can be divided into the *Epidendreae* (without stipes) and the *Vandeae* (with stipes).

9. The staminods in the Orchidales

Of the abaxial stamens $A_1 + a_1 + a_2$, only $a_1 + a_2$ are fertile in the *Apostasiaceae* and the *Cypripediaceae* (Plate I, Figs. 3A and 3B), whereas A_1 is fertile only in *Neuwiedia* (Plate I, Figs. 2A and 2B), but in their other genera A_1 is staminodial or completely wanting (as in *Adactylus*). That the fertile stamens belong to the inner or epipetalous whorl, follows from the fact that the vascular bundle, present in each of them, arises from the median vascular bundle of a lateral petal. The vascular bundle of A_1 arises from the bundle of the median sepal and so does the bundle of the staminode (A_1) in these two families, which element, therefore, belongs to the outer androecial whorl. I do not know if a corresponding (homotopic) vascular bundle occurs in *Adactylus*. The structure of the androecium is fairly clear in these two families, but rather obscure in the *Orchidaceae* s.s., especially if one wishes to maintain the pattern of $A_1 + a_1 + a_2$. The column only rarely bears thread-like protrusions reminiscent of stamens. However, laterally inserted organs (opposite the lateral petals) occur in various Australian genera, e.g., in *Diuris* and *Prasophyllum* (lacking a gynostemium, because style and stamen are free (the presence of pollinia and a rostellum determines their place in the *Orchidaceae* s.s.). A study of the possible relations between these lateral wings and the rudimentary stamens $a_1 + a_2$ was indicated. To this end I have examined transverse microtome sections. In both *Diuris* and *Prasophyllum* these wings appear to have a vascular bundle, and when one follows such a vascular bundle downwards, it appears that it is a derivative of the median vascular bundle of the lateral petals (Plate 2, Fig. 3A and 3B). From this one may safely conclude that these wings are the homologues of the stamens $a_1 + a_2$ and that they are indeed adnate staminodes.

Such distinct wings are very rare. In several other genera protrusions on the gynostemium have been recorded, such as the stelidia found in *Bulbophyllum ciliatum* (Bl.) Lindl. and in *Sobralia cataractarum* Hoehne. In certain genera the gynostemium sometimes has laterally protruding margins. An anatomical examination reveals that often these margins contain vascular bundles, also originating from the main vascular bundle of the lateral petals, in other words, these margins apparently represent the lateral stamens $a_1 + a_2$ and can be regarded as staminodes adnate to the column.

I have never observed corresponding vascular bundles in the *Orchidoideae*, but I did find them in representatives of the *Epidendroideae*, in both the *Neottianthae* and the *Epidendranthae*. In the *Neottianthae* I examined *Limodorum abortivum* (Plate III, Figs. 5A and 5B) and *Vanilla planifolia* (Plate III, Fig. 6). Among the *Epidendranthae* I noticed them in several genera, such as *Oncidium*, *Sophronitis*, *Cattleya*, *Aerangis* (Plate III, Fig. 7) and *Scaphyglottis*. No doubt they occur in a number of other genera as well. This strongly supports the assumption that also in the *Orchidaceae* subfamily *Epidendroideae* the gynostemium corresponds with that of the *Apostasiaceae* and the *Cypripediaceae*, and that, basically, it has incorporated the stamens $A_1 + a_1 + a_2$.

In several Eurasian genera of the *Neottianthae*, such as *Epipactis*, *Cephalanthera*, *Spiranthes* and *Goodyera*, neither wings nor thread-like protrusions on the gynostemium occur and only the three vascular bundles of the pistil and the one innervating A_1 are present. This is obviously a case of reduction. The reduction is even more pronounced in the *Orchidoideae* which have only two vascular bundles in the gynostemium, originating as offshoots of the vascular bundles of the median sepal; the one vascular bundle innervates the stamen A_1 and the other one the stigma and the rostellum (Fig. 15). The lateral stigmatic lobes do not contain vascular bundles. In some of the South African genera (*Disa*, *Satyrium* and other ones) there are indeed three vascular bundles in the pistil in addition to the bundle belonging to A_1. Apparently the gynostemium includes only the androecial element A_1. In the majority of the *Orchidoideae* and also in many *Neottianthae* the anther bears a small lateral appendage (auricle) on either side towards the base. It is these appendages which are frequently referred to as "staminodes" in taxonomic text books. This goes back to obsolete ideas expressed by Robert Brown and Eichler. These auricles, when anatomically examined, all appear to have a similar anatomical structure; they consist chiefly of large cells filled with crystalls (raphides). Animals with a sensitive tongue will not readily eat these organs and that is presumably why also the anthers are protected from being devoured by animals. Brown later questioned his own theory (1833, p. 697), because he had found a flower of *Platanthera* (*Habenaria*) *bifolia* with two supernumerary stamens. If the auricles are of staminodial derivation they must disappear as such when they are replaced by normal stamens. However, not only had the normal stamen in the abnormal *Platanthera* flower retained its auricles, but the extra stamens also bore an auricle at the side facing the normal stamen, in other words, these auricles apparently form a normal and integral part of the anther. Auricles also occur in *Allium*, *Ornithogalum* and *Deutzia*, for that matter. Eichler describes the auricles of the *Lauraceae* as "blosse stipulare Anhängsel der Staubblätter" ("mere stipular appendages of the stamens"). E. Capeder (1898, p. 42) describes a similar case in a flower with an additional stamen of *Orchis latifolia* and I have also observed a supernumerary stamen in *Dactylorchis* possessing an auricle, A_1 having retained this organ (Plate VI, Fig. 15) The auricles of the orchidaceous stamen are manifestly emergentia. Compare also Vermeulen (1953).

The question arises whether any remnants of the stamens $A_2 + A_3 + a_3$ can possibly be indicated. This seems most unlikely if we consider the style to be concrescent with the whole androecium, in other words, all stamens are likely to be connate as in the actinomorphic flowers of the *Aristolochiaceae*, *Nepenthaceae* and *Asclepiadaceae*. Some morphologists and taxonomists believe to have found the rudiments of the three missing stamens in the labellum (Darwin, Lindley). This seems improbable, because supernumerary stamens are always inserted on the gynostemium. Moreover, we may assume that the law of Dollo also applies to the orchid flower: *evolution is irreversible*. Supposing that the gynostemium was formed with the inclusion of $A_1 + a_1 + a_2$, we may assume that the other parts of the androecium had previously become reduced, and will always remain abortive. Elements of the perigone exhibit various differentiations, it is true, such as the lip in *Glossodia* and *Ophrys*, the lateral petals in *Dendrobium* and the median sepal of *Disa*. Brown suggested that the protrusion on the labellum of *Glossodia*, an Australian genus with about five species, would correspond with a_3 (Brown in Wallich, 1830, vol. I, p. 74; see also Verm. Botan. Schr., 1834, vol. V, p. 198; see Eichler, 1875, vol. I, p. 183, wrongly quoted by Eichler). To my mind this is nothing but a functional differentiation of the motile lip. This is even more evident in *Glossodia brunonis* Endl. = *Elythranthera brunonis* (Endl.) A. S. George, which possesses two similar protrusions on the base of the labellum (not on the column), which can move independently (see A. S. George, 1963, p. 4). *Epiblema grandiflorum* R. Br. has no less than half a dozen protrusions on the lip. The hypothesis that the lateral stamens ($A_2 + A_3$) are represented by the labellum is equally untenable, on similar grounds. This hypothesis is erroneously ascribed to Brown, both by Darwin (ed. 2, 1890, p. 237) and by Eichler l.c. However, Brown (in Wallich l.c.) stated: "It may be remarked that indications or rudiments of the two stamens necessary to complete the number in Orchideae of those namely, corresponding with the lateral segments of the outer series of the perianthium, have not yet been observed in the regular structure of any plant of that order". The hypothesis, in fact, dates back to LINDLEY who, in his work: The Vegetable Kingdom, ed. 3, 1853, p. 183, says: "In general the central of the outer whorl is alone perfect; while in Cypripedium perfection is confined to the lateral inner stamens. The rest of the stamens are either wholly suppressed, as in many Dendrobes, or appear in the form of ears to the column or crests upon the lip; the ears of the column sometimes representing the lateral inner staminodes, and the crests of the lip being made up either of the two lateral outer and one central inner staminode, or of either."

DARWIN, in his book on orchids (ed. 2, 1830, p. 236), shows a diagram to illustrate his contention that the stamens A_2 and A_3 became incorporated in the labellum. He founded his view on the course of the vascular bundle. The anatomical examination was repeated by B. G. L. SWAMY (1948). In his article: Vascular Anatomy of Orchid Flowers, this author draws the following conclusion (on p. 93): "The labellum is also shown to receive the same vascular supply as the rest of the perianth members; it is stressed that there is no evidence to consider it to be a compound structure, as was thought by Brown and Darwin." See also NELSON, 1965, p. 190.

In his splendid treatise on *Ophrys* and in his article: Zur organophyletischen Natur des Orchideenlabellums, Erich NELSON (1965), defends the view that the labellum of the orchids is compounded of the three stamens $A_2 + a_3 + A_3$, the median petal having disappeared. This hypothesis enables Nelson to identify the three lobes so often observed in the *Ophrys* labellum, e.g., in *O. cornuta* Stev. (=*O. scolopax* ssp. *cornuta* Lam.), with the three above mentioned missing stamens. The labellum in the species of the genus *Ophrys* often bears lateral protrusions. Yet, I do not suscribe to this hypothesis. My principal objections are the following:

If we assume that the highly evolved orchid flower, specialized in pollination by insects, can indeed be derived from the actinomorphous pentacyclic and trimerous Monocot flower, we must start from the simplest forms and not from the most specialized ones when assessing the homology of the various parts of the flower. Formerly, when interpreting the morphology of the higher plants, one started from the *Angiosperms* and the concepts of stem and leaf were extrapolated into the morphology of the lower plants. (See MEEUSE (1965): "Angiosperms — Past and Present".) One has since realised that this is the wrong way round and with the help of the telome theory one can now start with the simplest terrestrial plants, *Rhynia* and related genera, gradually to reach the specialized forms of the Angiosperms. When one wishes to interpret the most specialized forms of the orchid flower, in casu the flower of *Ophrys*, one should likewise start from the simplest flower, in which the lip differs very little in shape from the lateral petals and the zygomorphy is not yet manifest in the perianth. As soon as the homology of the lip of such a flower is determined, it will be possible gradually to determine the homology of the floral appendages of more specialized forms, starting from the simplest pattern, even if the various intermediate forms are not known.

In the *Apostasiaceae*, whose perianth is still fairly regular, only the elements $a_1 + A_2 + a_2$ of the androecium develop (Fig. 1A and 1B). The parts of the perianth, three sepaloid and three petaloid, occupy such a regular position that, to my mind, there is no reason whatsoever to consider the median petal a compound organ (see Plate I, Fig. 2A and 2B) of *Neuwiedia*. It follows from this figure htat three stamens have not developed:$A_2 + a_3 + A_3$. In the *Orchidoideae*, the genus *Herminium*, with many representatives in the Himalayas, also exhibits only a slight zygomorphy in its perianth. The gynostemium contains A_1 as the only fertile stamen. In this case there is, to my mind, not a single reason either to consider the labellum a compound organ. See KING & PANTLING (1898): The Orchids of the Sikkim-Himalaya, part IV, pl. 442, *Herminium orbiculare* Hook. fil. of which the labellum is almost ecalcarate. *Platanthera bifolia* Rich. also seems to provide a good starting point, even if the labellum in that species does have a spur. It is not always true that the labellum is the largest petal. In the South African genus *Disa* the labellum is sometimes very small and instead of the labellum the median sepal has a special form and is prolonged into a spur. It seems improbable that this median sepal could be a compound organ. Apparently zygomorphy can express itself in various directions. The fact that zygomorphy can evoke great differences becomes apparent from the conditions in the *Commelinaceae*, the species of the genus *Tradescantia* still having quite regular flowers, but the species of the genus *Commelina* exhibiting, not only in the androecium, but also in the corolla, a strong trend towards zygomorphy (*C. communis* L. with P_3 very small).

The morphology of flowers with anomalous and atavistic characteristics does not warrant the conclusion that the labellum is a compound organ, or that the median petal would be lacking. A number of cases is known in which supernumerary stamens $A_2 + A_3$ develop, (see BROWN, 1833) and in which the labellum develops quite normally. It often happens that a double lip develops, but this does not affect the morphology of the flower in any other respect. Being highly evolved *Ophrys* is a genus with many "adaptations", in particular as regards the lip. This may be concluded from the strange shape, the colour and the pubescence, which make the flower look like an insect or a spider. A similar resemblance not only occurs in representatives of the genus *Ophrys*, but also in several representatives of Australian genera. Edith Coleman has recorded the pseudo-copulation by male animals in those species. In Europe KULLENBERG (1961) carried out numerous experiments, from which it appeared that the *Ophrys* flowers by their shape, colour and smell apparently simulate female animals and thus induce the male animals to attempt a (pseudo-) copulation, by which they bring about the pollination. The lip of *Ophrys* is, to my mind, a strongly derived organ and that is why I think it incorrect to start from this form to determine the homology with a "standard" Monocot flower.

The following conclusions can be drawn:

1. In the orchids the labellum is a single organ, homologous

with the median petal of the *Monocotyledoneae* with regular flowers.
2. Evolutionary adaptations are responsible for the strongly specialized forms of orchid flowers, as in, e.g., *Ophrys*.
3. Consequently *Ophrys* is not a suitable object to serve as a starting-point for the assessment of the homology of the lip.

10. THE OVARY

The ovary in the *Orchidales* always contains three, often split (bifid) placentae and by a fairly general consensus of opinion, it is obvious to suppose that the ovary is composed of three carpels, on which the placentae developed marginally.

In the *Apostasiaceae* and in the genera *Phragmopedium* and *Selenipedium* of the *Cypripediaceae* the fruit is trilocular, in *Cypripedium* and *Paphiopedilum*, and in the *Orchidaceae* s.s. we find "parietal" placentae.

John LINDLEY (1853, p. 175) defended a different opinion; he thought there would be three fertile carpels bearing the placentae and three sterile ones bearing the stigmas apically. The traditional point of view is that there are sterile strips of tissue in the ovary enabling the fruit to open with six fissures (replum) but this does not imply that these three strips represent carpels. Accordingly, three carpels are drawn in the diagrams with marginal placentae (EICHLER, 1875, vol. I. p. 180; PULLE, 1952, ed. 3, p. 199). Nevertheless EICHLER op. cit., p. 182) says: "Yet the wall, as a rule, appears as if consisting of six, alternatingly sterile and fertile, carpels externally divided by grooves and internally by indistinct strips of tender tissue, of which the three fertile ones stand opposite the petals".

On the same page he reproduced some figures, adapted from LE MAOUT et DECAISNE, representing the six parts with the placentae in the middle (laminal) of the three fertile carpels. E. PFITZER in his Morphologische Studien über die Orchideenblüthe, 1886, p. 9 etc., discussed the structure of the gynostemium more exhaustively and mentioned a number of examples.

My attention was drawn to the problem of the structure of the ovaries in the *Orchidales* by the study of microscopic slides and by several drawings in the literature of orchids, e.g., those made by Madelle A. CAMUS, 1929: Iconographie des Orchidées, texte p. 126 by V. A. PODDUBNAYA-ARNOLDI, 1960: Akad S.S.S.R., vol. VI, table I: *Cypripedium* insigne; and by Leslie A. GARAY, 1960: On the origin of the Orchidaceae, plate IX? figs. 4 and 6, and various figures scattered in the older literature (e.g., in EICHLER, 1875, vol. I, Bluthendiagramme, p. 182). In all these figures the ovary is clearly reproduced as composed of six parts. My own observations of microscopic slides repeatedly indicated the same pattern of three parts bearing the (split) placentae alternating with three sterile parts. I saw this structural pattern in e.g. *Disa uniflora* (Plate IV, Fig. 10) *Schizodium inflexum* (Plate IV, Fig. 11), *Traunsteinera globosa*, *Caladenia spec.* (Plate IV, Fig. 12), *Epipogium aphyllum*, *Limodorum abortivum*, *Microtis parviflora*, *Thelymitra rosea* and *Aerangis coreacea*.

I was much astonished to see in the ovary of *Neuwiedia veratrifolia* also three laminal placentae and not a trilocular ovary as expected. Here too, especially in the young flower bud, I found six parts. The three hypopetalous parts have double placentae which are so large that they touch each other. This gives the impression as if the ovary is trilocular (Plate IV, Fig. 9) and later on this is, indeed, the case (in older flowers and in the fruit). I suppose that in the genera *Apostasia* and *Adactylus* we may find the same development. It also struck me that in the ovary of a *Cymbidium* hybrid, which I examined some time ago, six parts could so clearly be distinguished on the outside: three zones of the ovary wall converge apically and bear the sepals and these hyposepalous parts alternate with narrower hypopetalous zones bearing the placentae in their median portions and lying below the petals. This is rather suggestive of stachyospermy and would imply that the narrow placentae acquired foliaceous lateral outgrowths.

Lindley, the principal opponent of Robert Brown, was the first to submit the thesis that the ovary of the orchids consists of six parts. Brown, under the spell of the conception that the basic structural pattern of the orchid flower consists of regularly alternating trimerous whorls, opposed this idea. Brown's conception became almost universally accepted, but this is rather unfortunate in my opinion. In all modern hand books in which a floral diagram of the orchid flower is shown, the flower is always drawn as if there are only three carpels with marginal placentae.

An analogous problem occurs in those *Brassicales* (*Rhoeadales*) which have fruits dehiscing by means of two valves. In *Eschscholzia californica* we find a collar under the calyx (later under the fruit) and more distally a deciduous bipartite calyx, two dimerous whorls of petals, numerous stamens, and a tetramerous superior ovary with two long stigmas and two slighter shorter ones. There are only two placentae, so that also half of the component parts of the ovary are sterile. In *Glaucium flavum* and in *Chelidonium majus* (*Papaveraceae*) two valves fall off when the fruit ripens, and a frame formed by the two extremely narrow placentae remains. Similar cases are found in the *Fumariaceae*, e.g., in *Corydalis*. In the *Cruciferae* the valves are sterile and the narrow placental zones connected by the partition-wall persist (See HANNIG, Untersuchungen über die Scheidewände der Cruciferenfrüchte, Bot. Zeitung (1901) p. 207 et seq.)

The *Orchidales* exhibit a similar structure in their ovaries as we have seen but the gynoecium being trimerous, it has three sterile and three fertile parts. As in *Brassicales*, the placentae are split (bifid) and often even branched. The collar in *Eschscholzia*, present under the superior ovary, has an analogon in the calyculus found in some orchidaceous genera (*Epistephium*, *Lecanorchis*, *Neobenthamia* (Fig. 16) near the top of the ovary below the calyx and apparently associated with epigyny. We may accept, at least theoretically, that the receptacle extends to the top of the ovary, even if it is impossible clearly to distinguish the receptacle from the other component parts of the ovary. I think that the placentae of the *Orchidales*, unlike those of the *Cruciferae* (which grow

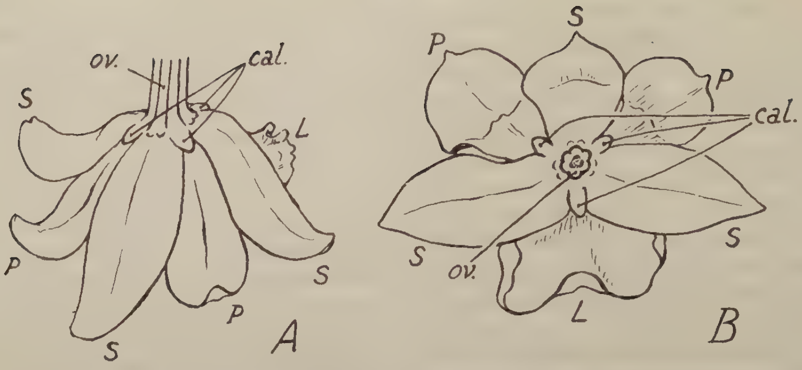


Fig. 16. Flower of *Neobenthamia gracilis* Rolfe to show the calyculus on top of the ovary below the sepals. cal.: calyculus; ov: ovarium; s: sepals; p: petals; l: lip.

centripetally to form the "false" septum), extended laterally to form the epipetalous zones of the ovarial wall. In addition one must assume that the receptacle is trifid, the fundamentally stachyospermous but secondarily foliaceously enlarged placentae having squeezed themselves in between the lobes of the receptacle as it were. The ovaries of several species of orchids indeed suggest that the hypopetalous zones are situated slightly below and between the hyposepalous portions. Sometimes the hyposepalous areas are apically connivent to form a ringshaped structure overlying the intervening apical portions of the placentiferous zones. This assumption is also quite compatible with the occurrence of a rim-like calyculus in the zone of insertion of the sepals (a condition which is the perfect parallelism of the development of a collar-like calycule in *Eschscholzia*). In the face of so much factual evidence, the conventional interpretation of the orchidaceous ovary as a tricarpellate structure with marginal placentation is untenable. The orchidaceous gynoecium consists of three sterile elements supporting the sepals and the pollen-receiving organs (the functional stigmas) alternating with the ovuliferous elements bearing the laminal double placentae (which are strongly ramified, apparently as a secondary adaptation associated with the very numerous ovules). Accordingly, the ovary must be interpreted as a hexamerous aggregate of two alternating whorls of three elements. This structure is suggestive of a stachyosporous condition, the ovules being produced on seed-bearing cauline organs secondarily connate with enveloping foliar elements. It may be significant in this connection that according to Payer the ovules do not develop simultaneously but successively on the placenta. Conceivably this mode of development is attributable to stachyospermy.

11. Stigma and Rostellum

The *Apostasiaceae* have three small stigmatic lobes, the *Cypripediaceae* have three large, distinct stigmas, alternating with the ovuliferous placentae. It has repeatedly been suggested that in the *Orchidaceae* the third stigmatic lobe became transformed into the rostellum, in other words, that only two stigmatic lobes are present. However, the examination of microscopic cross sections of the style and the stigma proves this view to be wrong: see the report of my lecture delivered during the I.B.C. in Paris (1954). In the *Orchidoideae* three stigmatic lobes can be frequently distinguished (*Dactylorchis*, *Disa*, *Himantoglossum*, *Orchis*, *Platanthera* (Plate III, Fig. 8A)), of which the median lobe is well developed. In various genera a reduction of the median stigmatic lobe took place (in *Gymnadenia*, *Anacamptis*) and in some genera the median stigmatic lobe has even disappeared altogether (in *Bonatea*, *Habenaria* s.s.) which is concomitant with an increase in size of the rostellum, which may even become quite large. As regards the connection between the rostellum and the stigma the reader should consult my earlier paper on the subject (VERMEULEN, 1959). In the last two genera the functional stigmatic lobes are born on a pair of stigmaphores.

The *Epidendroideae* often also possess three stigmatic lobes of which the median one not rarely bears the rostellum apically, the latter becoming secondarily attached to the stipe. In the *Neottianthae* the rostellum sometimes takes the place of the entire median stigmatic lobe, e.g., in the Australian genus *Pterostylis* and in *Zeuxine* from Africa and S. E. Asia. In most genera, however, there are three stigmatic lobes although it is often difficult to distinguish them in the maturing stigma because of an excessive secretion of a mucilaginous substance. The presence of three lobes is often indicated by the situation of the stylar canal, viz. in the centre of the stigma and not immediately beneath the rostellum as one would expect in the alternative case.

In the *Orchidoideae* the rostellum develops as a strap-shaped body with at either end a viscid disc, originally situated above the lateral stigmatic lobes (Plate III, Fig. 8B). In the *Epidendroideae* the rostellum develops as a single compact organ representing a part of the third stigmatic lobe (Plate II, Fig. 5B), or even replacing it entirely. In the group of the *Vandeae*, an important part of the rostellum is formed by the so-called stipe. This organ is always considered to be a derivative of the rostellum. It is often developed as a rather bulky organ and if this is the case it does not only form a part of the third stigma lobe, but also contributes largely to the tissue situated above the clinandrium. The polymorphous and functionally diversified stipe connects the rostellum proper with the pollinia. It gives the impression of being a separate piece of tissue derived from the gynostemium.

A remarkable form of rostellum, derived from the anther, I discovered in the Asiatic genus *Stereosandra*, of which spirit material from Thailand had been put at my disposition by Mr. G. Seidenfaden, Kopenhagen. In this genus the stigma does not at all participate in the formation of the rostellum, the latter being formed by a protruding part of the anther which subsequently excretes viscid matter (Plate VI, Fig. 14). The caudicles lie beneath this rostellum. Each caudicle consists of two converging strands, each of which forming a part, situated in the partition wall between the two loculi. The caudicle being formed by two such strands, it can not possible be a derivation of one of the pollen masses, even though it is ultimately located on top of the pollinia. As in *Epipogium*, the androecial bundle divides itself into three branches of which the middle one innervates the "rostellum" (See VERMEULEN, 1965).

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BOOK REVIEW

A. G. Voorhoeve, Liberian High Forest Trees. A systematic botanical study of the 75 most important or frequent high forest trees, with reference to numerous related species. Agricultural Research Reports 652, 1965. 416 pp., 72 figs.

Dr. Voorhoeve's book on Liberian high forest trees contains 72 full-page figures, showing in detail the botanical characters of more than 70 species, while of some dozens more details are added in order to render easy identification of species not specially treated in the book. The drawings are firm and clear, delicately executed and rank among the best published in recent years. Detailed descriptions accompany the figures, careful taxonomical notes explain the adopted delimitation and distribution of each species. Ecological data, field notes, the general aspect of each tree and information important to foresters (slash, bark, wood, silviculture) are given. There are 32 full pages photographs of trunk habits. These large scale photographs are highly valuable as a means of identification on the spot and very instructive to beginning foresters. As a rule one finds in forester's flora's small size photographs, which fail to convey the essentials to those not familiar with the species. These are exactly who need them most and, I presume, possibly later authors on similar subjects will try to convince publishers to reproduce illustrative photographs in a format as found in Dr. Voorhoeve's book.

Actually the book is full of new facts and observations. Dr. Voorhoeve studied during three years the Liberian forest on the spot and assembled or verified the data contained in the scarce literature on Liberian forests. Back in Europe, he completed his research by 1½ years of study in the Laboratory for Plant Taxonomy and -Geography in the University of Agriculture at Wageningen.

The result is a book for the Liberian forester, or for any professional worker concerned with Liberian forests, which will prove a rich source of reliable information.

It is not usual in forest flora's that type specimens are studied. Dr. Voorhoeve checked all species treated with type material and considered nomenclatural problems whenever this seemed advisable. As a result all accepted names rest on verified types.

A chapter on geography (map!) and climate (isohyetals mapped) and a general survey of the vegetation further add to the scope of "Liberian high forest trees".

Keys on foliar characters guide to the species; they are simple and easy to understand. They were successfully tried by forestry students before publication.

A glossary of terms, and figures illustrating the shapes of leaves further aid students with little practical experience on their way of recognizing the main trees.

Liberian High Forest Trees evidently is the best book on the subject now available and likely to remain so, it would seem, for many years to come.

H. C. D. de Wit

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Proceedings of the Feldafing Summer School, September 1964

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Acta Botanica Neerlandica **15** (1966) 255–265

A PALYNOLOGICAL STUDY IN COCOID PALMS

W. PUNT AND J. G. WESSELS BOER
(*Botanical Museum and Herbarium, Utrecht*)

(*received October 23rd, 1965*)

INTRODUCTION

Because the palm family is almost entirely tropical with many species of a very great size, it has attracted only a few botanists to study them. As a consequence palms are poorly represented in herbaria and little understood in almost every respect. Notably their taxonomy is in a very poor condition since many taxa are described on inadequate material which allows only an arbitrary interpretation and, moreover, the family is grossly overnamed. Hence the second author (1965) proposed a large-scale lumping in his critical treatment of the Suriname palms. The present paper is intended to give some palynological evidence to support a few of these lumpings on the generic level.

Palynological evidence shall especially be rewarding in the genus *Attalea* in the broad sense inclusive of *Maximiliana*, *Markleya*, *Orbignya*, *Parascheelea* and *Scheelea*. These genera have been separated on the morphology of the staminate flowers only; no correlation with other characters could be worked out in a satisfactory way. Apart from the very distinct staminate flower types representing *Attalea*, *Maximiliana*, *Orbignya*, and *Scheelea*, in recent times also a few intermediate flower types have been found, again evaluated as separate genera: *Markleya* and *Parascheelea*. The main argument for accepting these single character genera is a feeling that the evolution of the staminate flowers in the palms has been very extraordinary. If this feeling is correct, it may be expected that the differences in the staminate flower morphology run parallel with the differences in the pollen morphology. To check this was one of the purposes of the investigation the results of which are presented in this paper.

Also the pollen morphology of the genus *Elaeis* in the broad sense was studied. The three species belonging to this genus have been separated into three monotypic genera based on very poor morphological evidence and these, consequently, were not accepted by the second author (1965).

Finally, a superficial exploration was done in the group of prickly Cocoid palms, referred to a separate group of Bactroid palms by TOMLINSON (1961).

As both groups resemble each other so much in several respects it is interesting to learn if this anatomical separation is in agreement with the pollen morphology.

Herbarium material has been used from the Botanical Museum and Herbarium, Utrecht (U), collection Wessels Boer. The investigation was also based on a large duplicate set of slides from the slide collection of the Shell Research N.V., which N.V. was so kind to supply these slides. Material from which this set was prepared was largely obtained from the herbaria at Berlin (B) and Genève (G).

Descriptions have been made with the aid of a Leitz Ortholux microscope, apochr. obj. × 63, × 90 and an eye piece × 10. Photographs were made with the same microscope and lenses in combination with a Leitz Orthomatcamera. The magnification of the drawings and photographs are given in the text.

Pollen morphology

Up till now only few publications on the pollen grains of palms have been published. The largest number of descriptions is found in Erdtman's book "Pollen Morphology and Plant Taxonomy" (1952). He described among others the pollen of *Attalea princeps*, *Cocos nucifera*, and *Maximiliana venatorum*. *Elaeis guineensis* was examined by Zeven (1964), and Nair and Sharma (1963) studied the variability of the pollen grains in different varieties of *Cocos nucifera*.

The following groups of characters are important in describing pollen grains: 1. the apertures, 2. the shape, and 3. the exine.

1. *The apertures*

Two different kinds of apertures have been observed in palm pollen: a) pollen grains with 1 colpus, the monocolpate grains, and b) pollen grains with a threeslit colpus, the trichotomocolpate grains. These apertures are situated at the distal part of the grain (Erdtman, 1952).

Most species have grains that show monocolpate grains only, e.g. *Attalea cohune*, *Attalea tessmannii*, and *Scheelea dryanderae*. Several species are a mixture of both kinds of apertures. However, in each of these species monocolpate grains prevail, e.g. *Attalea insignis* and *Attalea sagotii*. In *Attalea maripa* 1) trichotomocolpate grains occur frequently and *Attalea oleifera* has trichotomocolpate grains only.

The two kinds of apertures are not likely to be of much taxonomical value.

Altogether there seems to be a trend, that trichotomocolpate grains occur less frequently in the Orbignya type (*Attalea sagotii* only) than in the Scheelea type (most species of this type).

2. *The shape*

The shape of the grain depends upon the kind of aperture. Trichotomocolpate pollen grains are regular triangular. Monocolpate grains are oblong or oval and usually asymmetric. The longest axis of the grain coincides with the length of the colpus. The largest breadth is usually found not in the middle, but shifted towards one end of the

---

1) The name *Maximiliana regia* is illegitimate as it is a later homonym of the Bixaceous *Maximilianea regia*. The combination *Attalea regia* (Martius) W. Boer (1965) is antedated by *Attalea maripa* (Correa de Serra) Martius, based on *Palma maripa* Correa de Serra, Ann. Mus. Hist. Paris 8: 75.1806. Aublet's use of "*Palma maripa*" cannot be considered to be more than a listing of a vernacular name.

pollen grain. Some species in the Scheelea type, in fact those with a very thick exine, have a more rectangular shape. In equatorial view (transverse position, ERDTMAN, 1952) the pollen grains are kidney shaped.

3. *The exine*

The exine is very important and provides the most constant characters. In palm pollen three layers can be distinguished with a light microscope: a) the capita-layer, b) the columellae-layer, and c) the endexine.

a) *capita-layer.* The capita are fused to a tectum which is still perforated (tectum perforatum). The fused capita may form different structures. In the Scheelea type patches sometimes are formed. In the Orbignya type the fusing of the capita results in vermiculate streaks, but in the Maximiliana type the fusing does not give rise to any special pattern. Sometimes the capita are fused laterally only, thus forming a reticulum. This structure is seen in *Attalea tessmannii.*

b) *columellae-layer.* Columellae support the tectum. These elements can be low or high and distinct or indistinct.

c) *endexine.* Except for its thickness this layer is not differentiated any further.

In the description of the wall of pollen grains we refer to the proximal side of the grain. The thickness of the exine is less at the distal side where the aperture is situated and here the structure is usually fainter or is even missing.

POLLEN TYPES IN ATTALEA *s.l.*

Maximiliana type

Monocolpate, sometimes trichotomocolpate.
Exine rather thick, from 1,5 to 3 μ. Tectum perforated, undulating.
Perforations numerous, irregularly arranged.
Capita indistinct, fused. Structure indistinct; sometimes indistinct patches visible.
Columellae distinct but low. Endexine thin.

(Fig. 1)

Scheelea type

Monocolpate, sometimes trichotomocolpate
Exine thick, from 2 to 6 μ.
Capita indistinct, fused, sometimes forming distinct patches, but usually indistinct pattern. Tectum perforated. Perforations few, in some species scattered, in other species in strings.
Columellae distinct, low. Endexine usually thick.

(Plate I C, D)

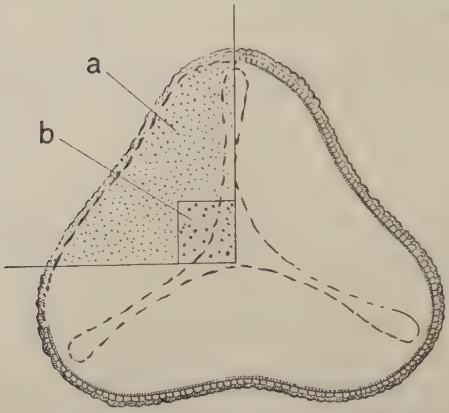


Fig. 1. *Attalea maripa* (Correa de Serra) Martius. Proximal pole; a. columellae layer; b. tectum with perforations.

Orbignya type

Monocolpate, rarely trichotomocolpate.
Exine thin or rather thick, from 1 to 2,5 μ.
Capita distinct, fused, forming vermiculate streaks. Tectum perforated, undulating. Perforations numerous, often in chains.
Columella distinct or indistinct, low. Endexine thin. **(Fig. 2)**

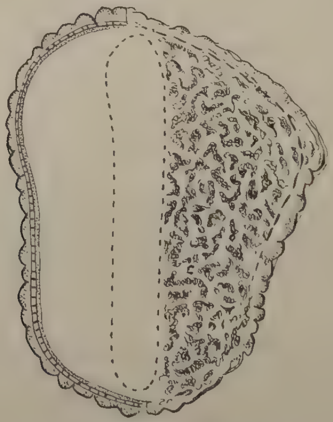


Fig. 2. *Attalea cohune Martius*

Description of the species

Attalea attaleoides (Barb. Rodr.) W. Boer Wessels Boer 1430 (U)

Monocolpate, longest axis ca 65 μ. Exine thick, ca 4 μ. Capita indistinct, fused. Tectum undulating, perforations in tectum rather crowded, sometimes in short chains. Columellae low, distinct. Endexine thick. *Scheelea type.*

Attalea cohune Martius
Sentle 3234 (B)
Glaziou 16468 (B)

Monocolpate, longest axis ca 60 μ. Exine ca 2 μ. Capita distinct, fused in vermiculate streaks. Tectum undulating, perforations in tectum many. Columellae low, distinct. Endexine thin. *Orbignya type.*

Scheelea dryanderae Burret
Dryander XII (type) (B)

Monocolpate, longest axis ca 60 μ. Exine thick, 2,5–3,5 μ. Capita indistinct, fused, forming distinct patches. Tectum undulating, perforations in tectum rather few, in chains. Columellae distinct, rather high. Endexine rather thin. *Scheelea type.*

Attalea dahlgreniana (Bondar) W. Boer **Plate II B, C**
Wessels Boer 805 (U)

Monocolpate, longest axis ca 50 μ. Exine thin, 1,5–2 μ. Capita indistinct, not fused in a distinct pattern. Tectum undulating, perforations in tectum crowded. Columellae low, indistinct. Endexine thin. *Maximiliana type.*

Attalea insignis (Martius) Drude **Plate I C, D**
Krukoff 5622 (G)
Johnstone 1577a (B), 1573 (B)

Monocolpate, sometimes trichotomocolpate, longest axis ca 65 μ. Exine thick, 4–6 μ. Shape slightly rectangular. Capita fused, forming distinct patches. Tectum undulating, perforations in tectum few, sometimes in chains. Columellae low, distinct. Endexine thick. *Scheelea type.*

Scheelea leandroana Barb. Rodr. x *S. huebneri* Burret Johnstone 1845 (B).

Monocolpate, longest axis ca 65 μ. Exine thick, 2–3 μ. Shape slightly rectangular. Capita indistinct, fused, forming patches. Tectum undulating, perforations in tectum few. Columellae low, distinct. Endexine thick. *Scheelea type.*

Parascheelea luetzelburgii (Burret) Dugand Luctzelburg 21969 (type) (B)

Monocolpate, longest axis ca 65 μ. Exine thick, 4–5 μ. Capita indistinct, fused. Tectum undulating, perforations in tectum few and scattered. Tectum much thicker than endexine. Columellae low, distinct. Endexine thin. *Scheelea type.*

Attalea macropetala (Burret) W. Boer
Wessels Boer 1330 (U)

Monocolpate, longest axis ca 40 μ. Exine ca 2 μ. Capita fused into a tectum, indistinct. Perforations indistinct, many, not forming a distinct pattern. Columellae low, indistinct. Tectum only slightly undulating. Endexine thin. *Maximiliana type.*

Attalea maripa (Correa de Serra) Martius **Plate I A, B**
Martius s.n. (G)
Wessels Boer 288 (U)
B. L. Meyer s.n. (?)

Monocolpate, sometimes trichotomocolpate, longest axis ca 55 μ. Exine rather thick, ca 2,5 μ. Capita distinct, fused in an indistinct pattern of patches. Tectum undulating, perforations in tectum many. Columellae low, distinct. Endexine thin. *Maximiliana type.*

Attalea oleifera Barb. Rodr.
Glaziou 15556 (B)

Trichotomocolpate, longest axis ca 55 μ. Exine thin, 1,5–2 μ. Capita indistinct, indistinct pattern. Tectum undulating, perforations in tectum many. Columellae low, indistinct. Endexine thin. *Maximiliana type.*

Scheelea osmantha Barb. Rodr.
Johnstone 1854 (B)

Monocolpate, rarely trichotomocolpate, longest axis ca 70 μ. Exine thick, 2–3 μ.

Capita indistinct, fused. Tectum undulating, perforations in tectum few, scattered. Columellae low, distinct. Endexine thick. *Scheelea type.*

Attalea parviflora Barb. Rodr. Hassler 7165 (type) (G)

Monocolpate, longest axis ca 55 μ. Exine rather thin, ca 2 μ. Capita indistinct, fused, thus forming an indistinct pattern. Tectum undulating, perforations in tectum rather many, irregularly arranged. Columellae low, distinct. Endexine thin. Transition to Maximiliana type. *Scheelea type.*

Scheelea preussii Burret without collector s.n. (B)

Monocolpate, rarely trichotomocolpate, longest axis ca 60 μ. Exine thick, 3–3,5 μ. Capita indistinct, fused, forming distinct patches. Tectum undulating, perforations in tectum few, scattered. Columellae rather indistinct, low. Endexine thick. *Scheelea type.*

Orbignya cf. *sabulosa* Barb. Rodr. Huebner 74 (B)

Monocolpate, longest axis ca 45 μ. Exine thin, 1–1,5 μ. Capita distinct, fused in vermiculate streaks. Tectum undulating, perforations in tectum many. Columellae low, rather indistinct. Endexine thin. *Orbignya type.*

Attalea sagotii (Trail ex Im Thurn) W. Boer Wessels Boer 708 (U)

Monocolpate, sometimes trichotomocolpate, longest axis ca 50 μ. Exine rather thin, 1–1,5 μ. Capita distinct, fused in distinct vermiculate streaks. Tectum undulating, perforations in tectum many. Columellae low, rather indistinct. Endexine thin. *Orbignya type.*

Attalea spectabilis Martius **Plate II A** Wessels Boer 1365 (U)

Monocolpate, longest axis ca 50 μ. Exine thin, ca 1,5 μ. Capita distinct, pattern indistinct. Tectum smooth, only slightly undulating, perforations in tectum many, indistinct. Columellae low, indistinct. Endexine thin. *Orbignya type.*

Attalea speciosa Martius **Plate II D, E**
Cult. Hort. Bot. Georgetown (K)

Monocolpate, longest axis ca. 60 μ. Exine ca 2 μ. Capita rather indistinct, fused into slightly visible vermiculate streaks. Tectum undulating, perforations in tectum many. Columellae low and distinct. Endexine thin. *Orbignya type.*

Scheelea stenorhyncha Burret Tessmann 5256 (type) (G)

Monocolpate, sometimes trichotomocolpate, longest axis ca 65 μ. Exine thick, ca 5 μ. Capita indistinct, fused into a thick tectum, perforations in tectum few and scattered. Tectum much thicker than columellae and endexine, only slightly undulating. Columellae low, indistinct. Endexine thin. *Scheelea type.*

Orbignya urbaniana Dammer Glaziou 22265 (K)

Monocolpate, longest axis ca 55 μ. Exine thin, ca 1,5 μ. Capita distinct. Tectum smooth, only slightly undulating, perforations in tectum many, indistinct. Columellae low, indistinct. Endexine thin. *Orbignya type.*

Attalea tessmannii Burret Tessmann 5167 (type) (G)

Monocolpate, longest axis ca 70 μ. Exine rather thick, ca 2,5 μ. Capita distinct, laterally fused into a fine reticulum. Lumina narrower than 1 μ, transition to a tectum perforatum. Columellae long and distinct. Endexine thin. *Maximiliana type*?

Comment

Maximiliana type

Grains monocolpate, sometimes trichotomocolpate. The exine is varying in thickness, but does not exceed 3 μ. The capita are fused, thus forming a tectum which does not show a distinct pattern. Many perforations are visible. These perforations are not arranged in a special pattern. The columellae are usually low and indistinct.

To this type belong *Attalea maripa*, *Attalea dahlgreniana*, *Attalea macropetala*, and *Atttalea oleifera*.

Attalea oleifera resembles the Maximiliana type in structure but the grains are always trichotomocolpate. As the difference between monocolpate and trichotomocolpate grains does not seem to be of taxonomical value, this species is placed in the Maximiliana type.

Attalea tessmannii also resembles the Maximiliana type, but in this species the laterally fused capita form a distinct reticulum and, moreover, the columellae are exceptionally high. The columellae-layer is higher than the capita-layer or the endexine.

Scheelea type

The grains are usually monocolpate but sometimes trichotomocolpate grains are mixed with monocolpate grains. The most striking character is the thick exine. The capita are fused into a thick, massive tectum in which the number of perforations is smaller than in the other types. The perforations are sometimes arranged in chains. The chains are winding giving the surface of the grains a patchy appearance (*Attalea insignis*, *Scheelea dryanderae*). Other species have few perforations too, but these are scattered over the surface and do not form a special pattern. The columellae are usually distinct and low. The endexine often is thick.

To this type belong those species which most taxonomists distinguish as a separate genus *Scheelea*: *Attalea attaleoides*, *Attalea insignis*, *Attalea parviflora*, *Scheelea dryanderae*, *Scheelea leandroana* x *S. huebneri*, *Scheelea osmantha*, *Scheelea preussii*, and *Scheelea stenorhyncha*. *Orbignya luetzelburgii* (*Parascheelea luetzelburgii*) belongs also to this type.

In this type there is a transition from the typical Scheelea type into the Maximiliana type.

Scheelea type ————→ Maximiliana type
A. insignis – – → *S. dryanderae* – – → *A. attaleoides* – – → *A. parviflora*
S. leandroana x *S. huebneri*
S. osmantha
S. preussii
S. stenorhyncha

Orbignya type

Grains monocolpate, rarely trichotomocolpate. The exine is usually thin and its thickness never exceeds 2,5 μ. The capita are fused and form a tectum, but in contrast to the two other types they remain clearly visible. The perforations in the tectum are numerous and arranged in short vermiculate chains thus forming irregularly curved lines. The columellae are low and often indistinct. The endexine is always thin.

To this type belong those species which most taxonomists distinguish as a separate genus *Orbignya*: *Attalea cohune*, *Orbignya* cf. *sabulosa*, *Attalea sagotii*, *Attalea speciosa*, *Attalea spectabilis* and *Orbignya urbaniana*. In this type too it is possible to make a series of species showing transitions from the typical Orbignya type to the Maximiliana type.

Orbignya type ———→ Maximiliana type
A. cohune – – → *O.* cf. *sabulosa* – – → *A. sagotii* – – → *A. speciosa*
A. spectabilis
O. urbaniana

TAXONOMIC NOTES

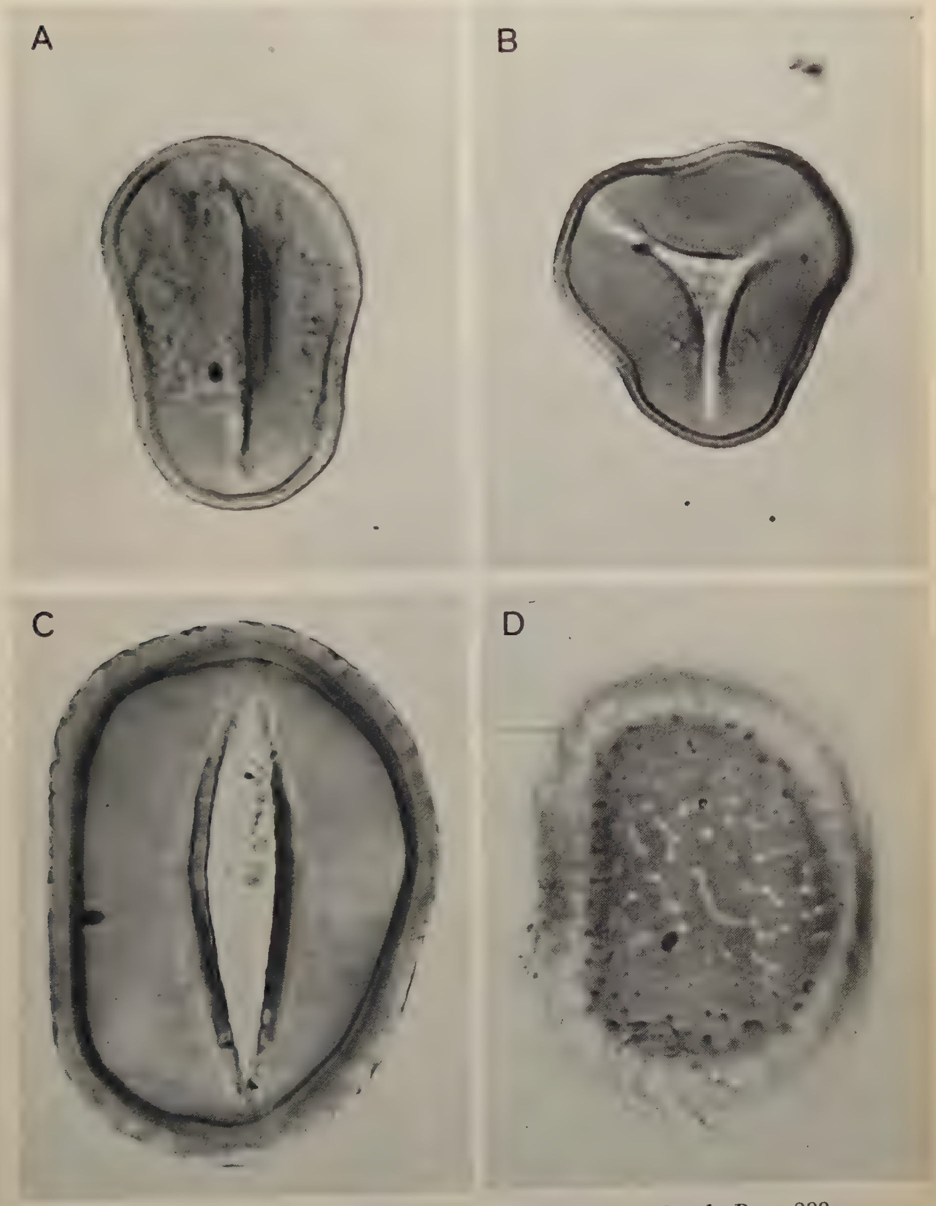
It can be seen from the foregoing that as well as there are different staminate flower types, there are also distinguishable pollen types. There is a tendency towards a correlation between staminate flower types and pollen types and, consequently, the pollen types have been referred to a Maximiliana, a Scheelea, and an Orbignya type. Unfortunately only two species of the genus *Attalea* in the narrow sense could be examined. These two species show marked differences and no generalization as to an Attalea type is reached.

According to BURRET (1929) *Attalea* s. str. is the most primitive genus from which *Orbignya* and *Scheelea* have been evolved. *Maximiliana* is supposed to be very close to *Scheelea*. Subsequently intermediates between *Orbignya* and *Scheelea* (*Parascheelea*), and *Orbignya* and *Maximiliana* (*Markleya*) have been described.

The intermediate staminate flowers of *Parascheelea luetzelburgii*, described by Burret in the genus *Orbignya*, contain pollen grains which match the Scheelea type exactly. The staminate flowers of *Attalea* (*Markleya*) *dahlgreniana* have pollen grains of the Maximiliana type. *Attalea* (*Maximiliana*) *attaleoides* has pollen grains belonging to the Scheelea type so that in this case the staminate flower type also concurs with the pollen type. The species was placed in *Maximiliana* on account of the fruit having superficial endocarp pores with a cover and without fibers. The same fruit characters were observed in *Attalea* (*Markleya*) *dahlgreniana* and *Attalea spectabilis*, both species with staminate flowers of the Markleya type. The examined *Attalea oleifera* also has the Maximiliana pollen type but not the Maximiliana fruit type. Obviously the Maximiliana pollen type is not restricted to the Maximiliana flower type nor correlated with the Maximiliana fruit type.

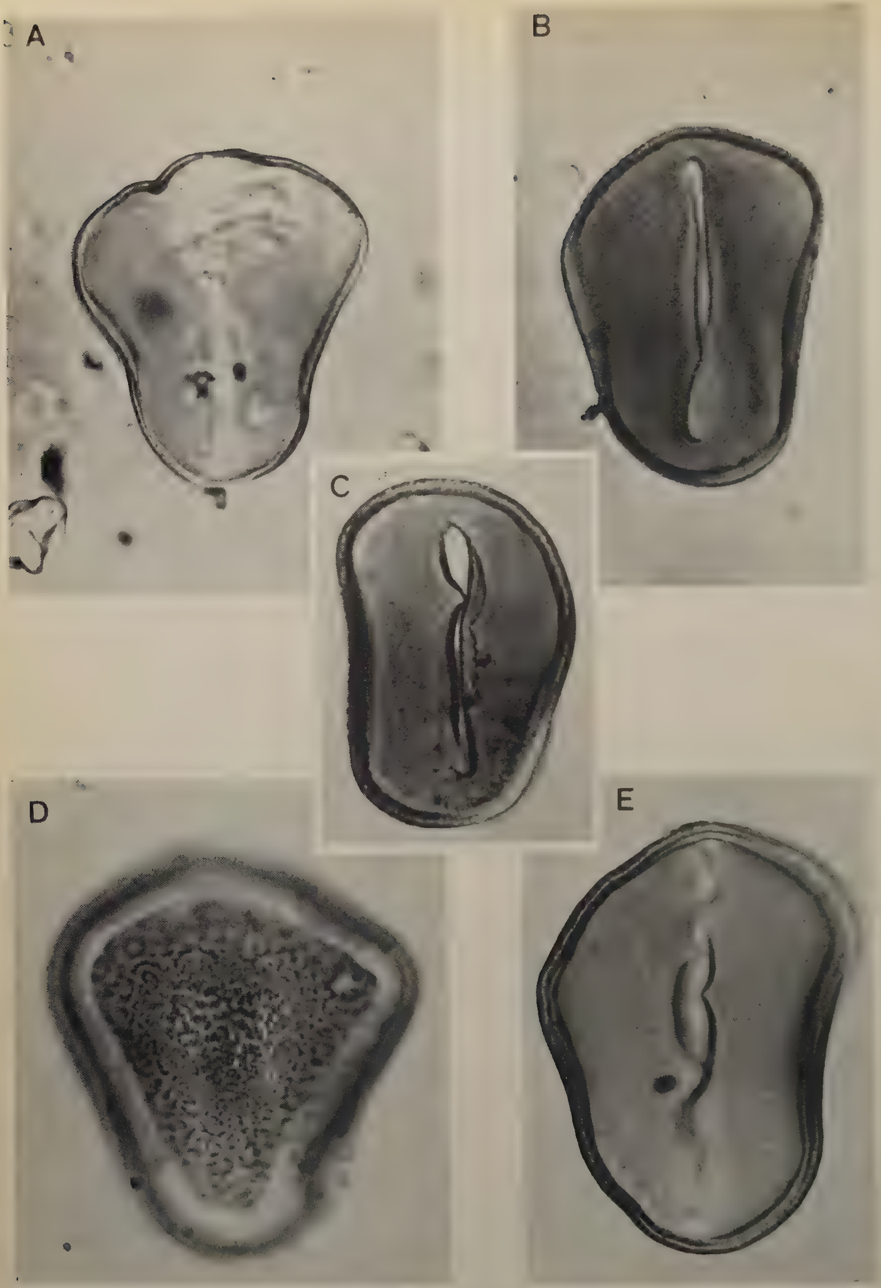
The torded and twisted anthers of the Markleya and the Parascheelea flower type remind one of the irregularly twisted and inrolled anthers of the Orbignya flower type. Nevertheless, these twisted anthers produce pollen grains of the Maximiliana, Scheelea, and Orbignya type respectively. Apparently the torded anthers do not provide a very reliable character.

On the other hand the pollen grains also show some intergradations between the distinguished types. *Attalea* (*Orbignya*) *speciosa* with staminate flowers of the Orbignya type has pollen grains intermediate



A. and B. *Attalea maripa* (Correa de Serra) Martius, Wessels Boer 288.
A. Monocolpate grains, B. trichotomocolpate grain, Krukoff 5622.
C. and D. *Attalea insignis* (Martius) Drude.
C. optical section, D. surface pattern.

PLATE I



A. *Attalea spectabilis* Martius, Wessels Boer 1365.
B. and C. *Attalea dahlgreniana* (Bondar) W. Boer, Wessels Boer 805.
B. tectum perforatum, C. optical section.
D. and E. *Attalea speciosa* Martius; Cult. Hort. Bot. Georgetown.
D. surface pattern, E. optical section.

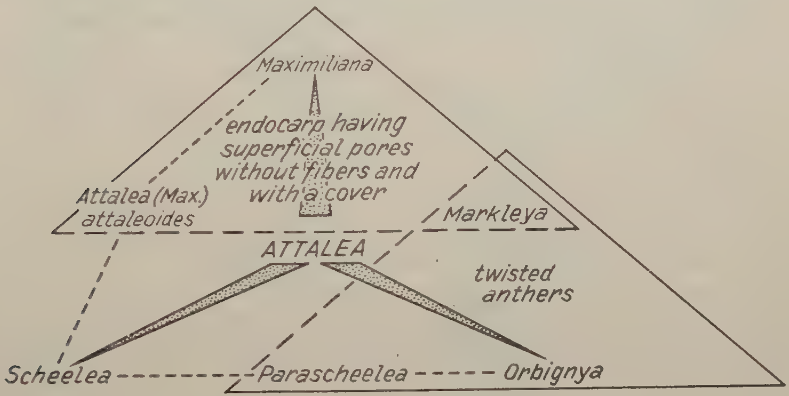
PLATE II

between the Maximiliana and Orbignya type. *Attalea* (*Scheelea*) *parviflora* with staminate flowers of the Scheelea type has pollen grains intermediate between the Maximiliana and Scheelea type.

Resuming we can state for the genus *Attalea* in the broad sense:

1. the pollen morphology does not allow to split up the genus into smaller groups notwithstanding the fact that different pollen types can be distinguished;
2. there is a rather strong but not absolute correlation between the pollen types and the staminate flower types.

As was done after the study of morphological characters alone, here again it must be concluded that the relationships among the species of the genus *Attalea* in the broad sense are so close in several respects that no satisfactory separation on the generic level can be worked out. The mutual relations are diagramatized in the scheme below.



Burret (1929) also proposed an infrageneric division: in *Scheelea* based on a character of the endocarp, and in *Orbignya* on the position of the staminate flowers on the rachillas. Both divisions proved to have no correlation with the differences found in the pollen grains. *Attalea* (*Scheelea*) *parviflora*, *Attalea* (*Scheelea*) *insignis*, and *Scheelea leandroana* are all placed in the section *Synalphocaryum*, but the first matches the Maximiliana pollen type quite well, whereas the second differs strongly from that, and the third takes an intermediate position. Also the examined species of the section *Dialphocaryum*, *Scheelea osmantha*, *Scheelea preussii*, and *Scheelea stenorhyncha*, represent such intermediates; *Scheelea dryanderae*, supposed to be closely related to *Scheelea stenorhyncha*, again differs more strongly from the Maximiliana type.

The species examined in *Orbignya* also show a series in the Orbignya pollen type towards the Maximiliana pollen type in which the extremes were placed in the section *Distichanthus*, the intermediates in the section *Pleiostichanthus*.

POLLEN GRAINS OF ELAEIS

Elaeis guineensis Jacq. Wessels Boer 1341 (U)
Trichotomocolpate, longest axis ca 40 μ. Exine thin, ca 1,5 μ. Tectum perforated, undulating. Perforations indistinct. Structure indistinct. Capita indistinct. Columellae low, indistinct. Endexine thin. Capita thinner than columellae and endexine together.

Elaeis oleifera (H.B.K.) Cortés (*Corozo oleifera*) Wessels Boer 155 (U)
Monocolpate, slightly asymmetric, longest axis ca 40 μ. Exine rather thick, 1,5–2 μ. Tectum perforated, undulating. Perforations many, indistinct. Structure indistinct. Capita fused, indistinct. Columellae low, indistinct. Endexine thin. Capita thicker than columellae and endexine together.

Elaeis odorata Trail (*Barcella odorata*) Froés 28315 (P)
Monocolpate, asymmetric, largest axis ca 50 μ. Exine thin, ca 1,5 μ. Tectum perforated, undulating. Perforations many, indistinct, sometimes in chains. Capita distinct. Columellae low, indistinct. Endexine thin. Faint structure present. Capita about as thick as columellae and endexine together. **(Fig. 3)**

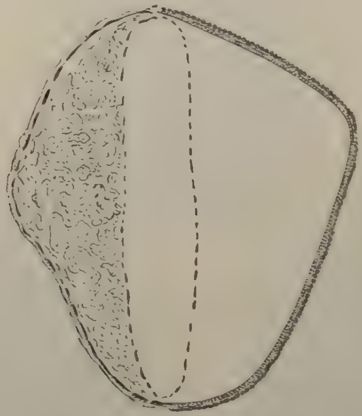


Fig. 3. *Elaeis odorata* Trail.

The pollen grains of the three *Elaeis* species do not show any distinct character which might separate them from each other or from other palm taxa. The exine is thin and is not clearly structured. The capita are irregularly fused to a tectum with many perforations.

The only difference is the shape. *Elaeis guineensis* is trichotomocolpate and the other two species are monocolpate. This difference is of minor importancy in the palm family only.

NAIR and SHARMA (1963) found monocolpate and trichotomocolpate grains in *Cocos nucifera* both in one specimen. ERDTMAN (1952) described this phenomenon in the species *Euterpe oleracea* and *Jessenia bataua*. In the genus *Attalea*, too, this dimorphism occurs. The three species do not differ much in size. *Elaeis guineensis* and *Elaeis oleifera* are almost of the same size, only *Elaeis odorata* is slightly smaller.

The exine is not very characteristic and therefore it is probable that palms in other groups of this family will show the same exine structure. *Elaeis odorata* only has an indistinct pattern. The surface is a little bit spotted.

TOMLINSON (1961) claimed a rather isolated position for *Elaeis* within the Cocoid palms. However, the uncharacteristic pollen grains do not provide much evidence for this and no separation either from the Cocoid palms nor from three distinct monotypical genera is supported by pollen morphology.

AN ADDITIONAL NOTE ON BACTROID PALMS

TOMLINSON (1961) separated the Bactroid palms from the Cocoid palms. The Bactroid palms have pollen grains which have only few characters in common with the three types from the genus *Attalea*. Examined species:

Astrocaryum vulgare Martius	Wessels Boer 314 (U)
Astrocaryum paramaca Martius	Wessels Boer 308 (U)
Astrocaryum sciophilum (Miquel) Pulle	Wessels Boer 327 (U)
Bactris elegans Barb. Rodr.	Wessels Boer 1591 (U)
Bactris gasipaes H.B.K.	Wessels Boer 520 (U)
Bactris maraja Martius	Wessels Boer 468 (U)
Desmoncus polyacanthos Martius	Wessels Boer 174 (U)

The pollen grains of *Acrocomia lasiospatha* Martius (Wessels Boer 1338) have some resemblance with the Scheelea type. The thick exine and the few perforations in the tectum agree with what is found in the Scheelea type. All grains, however, are trichotomocolpate, whereas those in all species in the Scheelea type are predominantly monocolpate.

These preliminary data seem to agree with Tomlinson's opinion that the Bactroid palms should be separated from the Cocoid palms.

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A PALYNOLOGICAL STUDY IN GEONOMOID PALMS

W. PUNT and J. G. WESSELS BOER
(*Botanical Museum and Herbarium, Utrecht*)

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INTRODUCTION

In a previous palynological study in Cocoid palms the present authors (PUNT and WESSELS BOER, 1966) were able to demonstrate a rather strong but not absolute correlation between the pollen types and the staminate flower types within the genus *Attalea* in the broad sense. The existence of partly apparently primitive, partly very advanced flower types within the otherwise close related group of Geonomoid palms made it worthwhile to investigate the same feature in this group.

The Geonomoid palms are usually considered to comprise 7–9 genera of monoecious Arecoid palms which share a large number of characteristics (BURRET, 1930; MOORE, 1966). The group is very obviously a most natural one. The generic distinctions are mainly based on the flower morphology, notably on differences found in the androeceum and pistil.

Staminate palm flowers in general have most frequently 2 whorls of 3 stamens, rarely 1 whorl is lacking or, more frequently, a larger number of stamens or many stamens are present. Usually the anthers consist of 2 lengthwise connected thecae, sagittate at base, dorsifixed and erect in bud. Sometimes rather far derived forms occur. The complete series is observed within the Geonomoid palms. *Welfia* and *Aristeyera* have many stamens per male flower (about 20–40); *Calyptrogyne*, *Calyptronoma*, *Pholidostachys*, *Asterogyne*, *Geonoma*, and *Taenianthera* have 6 stamens; *Kalbreyera* has only 3 stamens. Also the shape of the stamens differs much in the different genera. *Welfia*, as well as *Calyptrogyne*, *Calyptronoma*, and *Pholidostachys* have the above described dorsifixed sagittate anthers erect in bud (Fig. 1). A more unusual type of stamens occurs in *Asterogyne*, *Kalbreyera*, and *Geonoma*. These genera have stamens with separate thecae born on a bifurcate connective and forming, also at anthesis, a sharp angle with the filament (Fig. 2). This stamen type can be derived from the normal type by a hypothetical reduction of the upper part of the thecae (Fig. 3). The bifid connective is again much more developed in *Aristeyera* and *Taenianthera*, bearing separate thecae at its terminal end. This connective with the thecae is inflexed in bud and becomes erect, in line with the filament, at anthesis (Fig. 4).

The pistil of palms in general consists usually of 3 free or more or less united carpels. Also in Geonomoid palms a 3-celled ovary with a terminal style having 3 recurved style branches is found in most genera (Fig. 5). *Geonoma* and *Taenianthera*, however, form an exception.

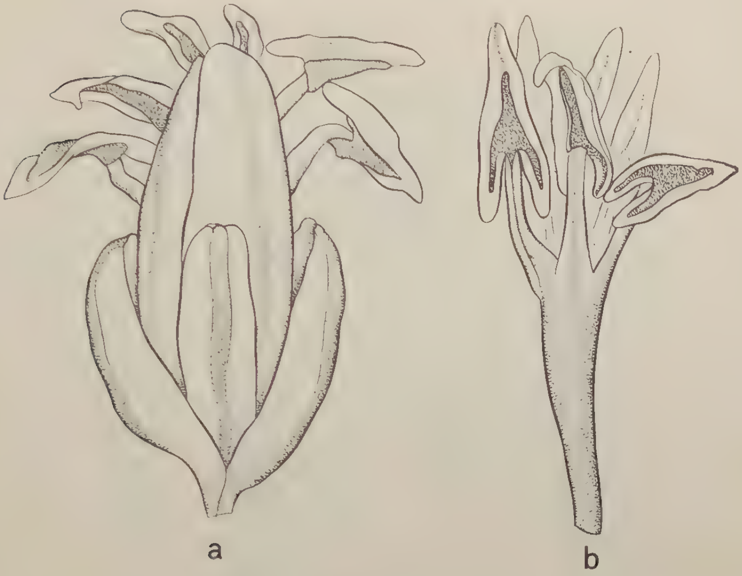


Fig. 1. *Calyptronoma occidentalis*
a. staminate flower; b. androeceum (Ekman H15685, Hispaniola).

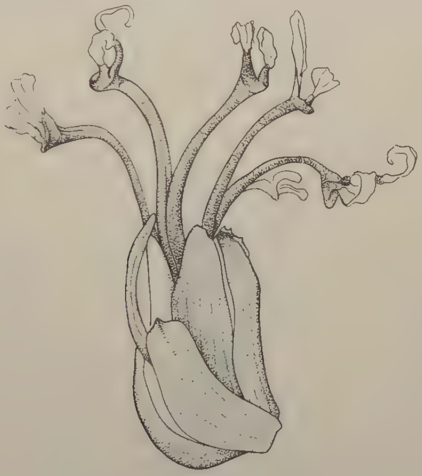


Fig. 2. *Geonoma baculifera*
Staminate flower (Killip 37437, Venezuela).

These genera have, by reduction of 2 locules, a 1-celled ovary with a basifixed style ending in 3 recurved style branches (Fig. 6). Also the degree of fusion of the staminodes in the pistillate flowers shows some variation. In most genera the staminodes are more or less connate at the base and free in the upper part (Fig. 5). In *Kalbreyera* and the majority of *Geonoma* species, the subgenus *Eugeonoma* of Burret, the

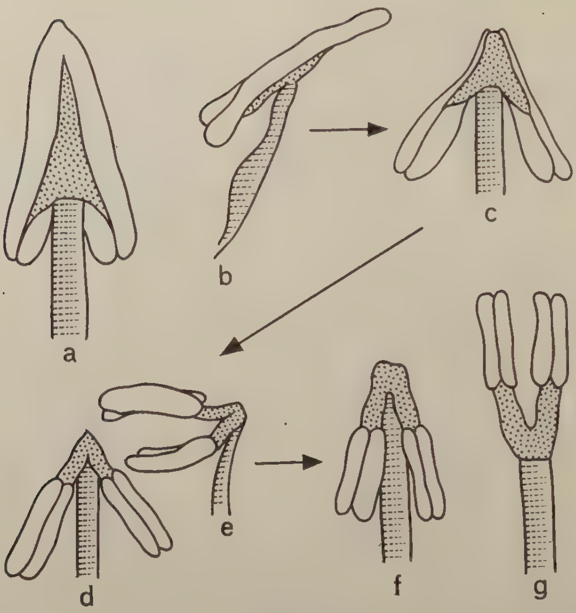


Fig. 3.
Scheme of the series of stamen types. a and b. Welfia type; c. theoretical intermediate; d. and e. Geonoma type; f. and g. Taenianthera type.

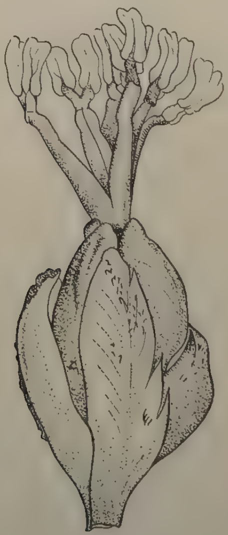


Fig. 4. *Geonoma* (= *Taenianthera*) *poiteauana*.
Staminate flower (Hulk 284, Suriname).

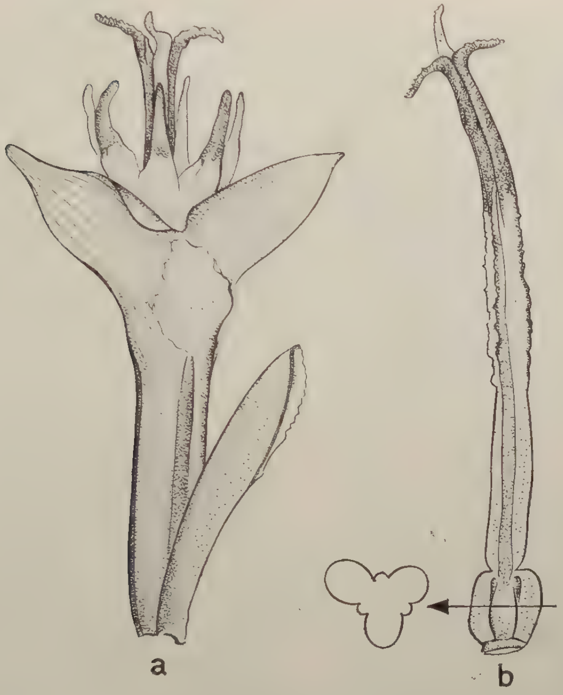


Fig. 5. *Asterogyne martiana*
a. pistillate flower; b. pistil (Englesing 350, Nicaragua).

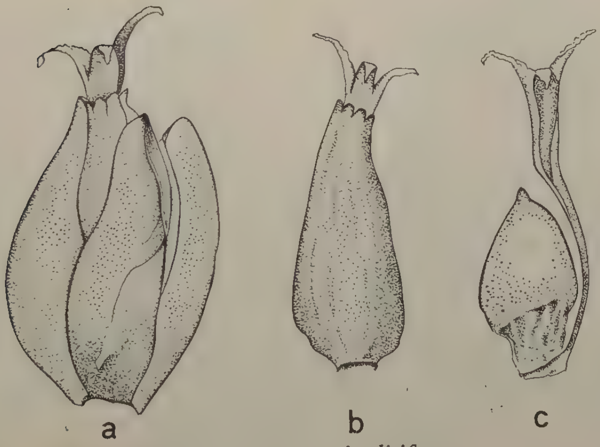
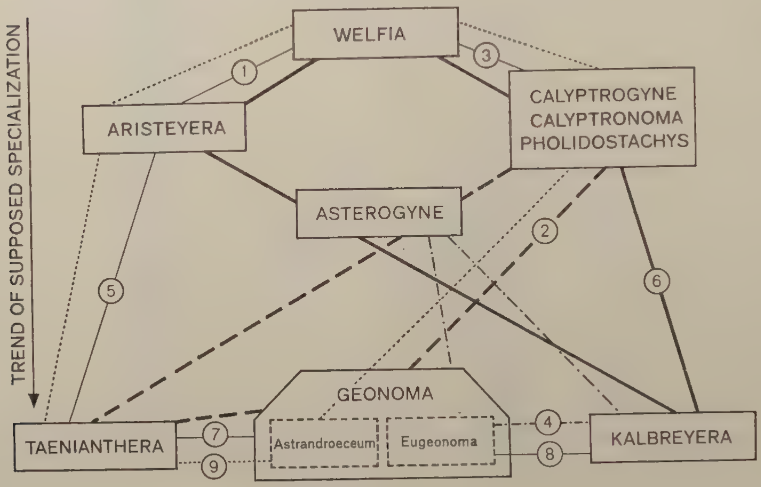


Fig. 6. *Geonoma simplicifrons*
a. pistillate flower; b. staminodial tube enclosing pistil; c. pistil (Killip and Lasser 37802, Venezuela).

staminodes are almost completely connate forming a truncate or slightly crenulate staminodial tube (Fig. 6).

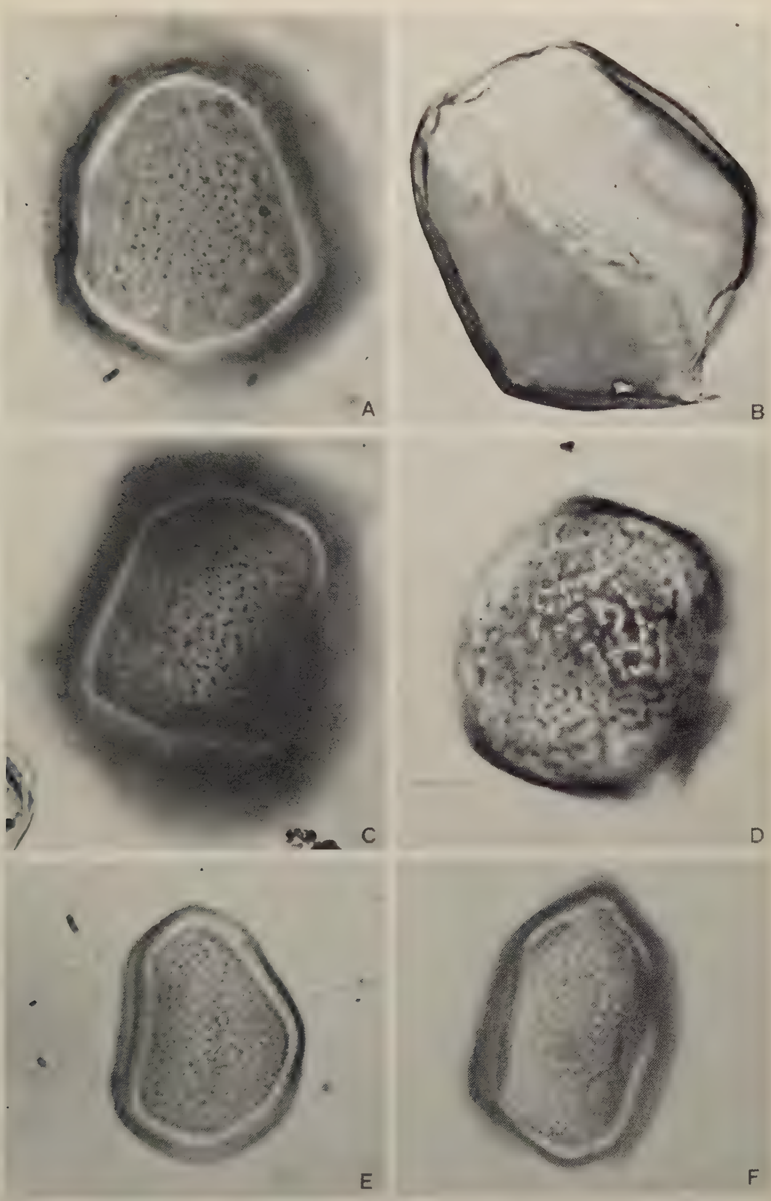
The occurrence of the different flower characteristics in the separate genera is visualized in the next scheme.



———①———	numerous stamens
— —②— —	6 stamens
———③———	dorsifixed sagittate anthers with connected thecae
.—.—④—.—.	free thecae at anthesis sharply deflexed
———⑤———	free thecae at anthesis in line with the filament
———⑥———	3-celled pistil
———⑦———	1-celled pistil
———⑧———	staminodial tube crenate or truncate
- - - - ⑨ - - - -	staminodial tube digitate or lobate

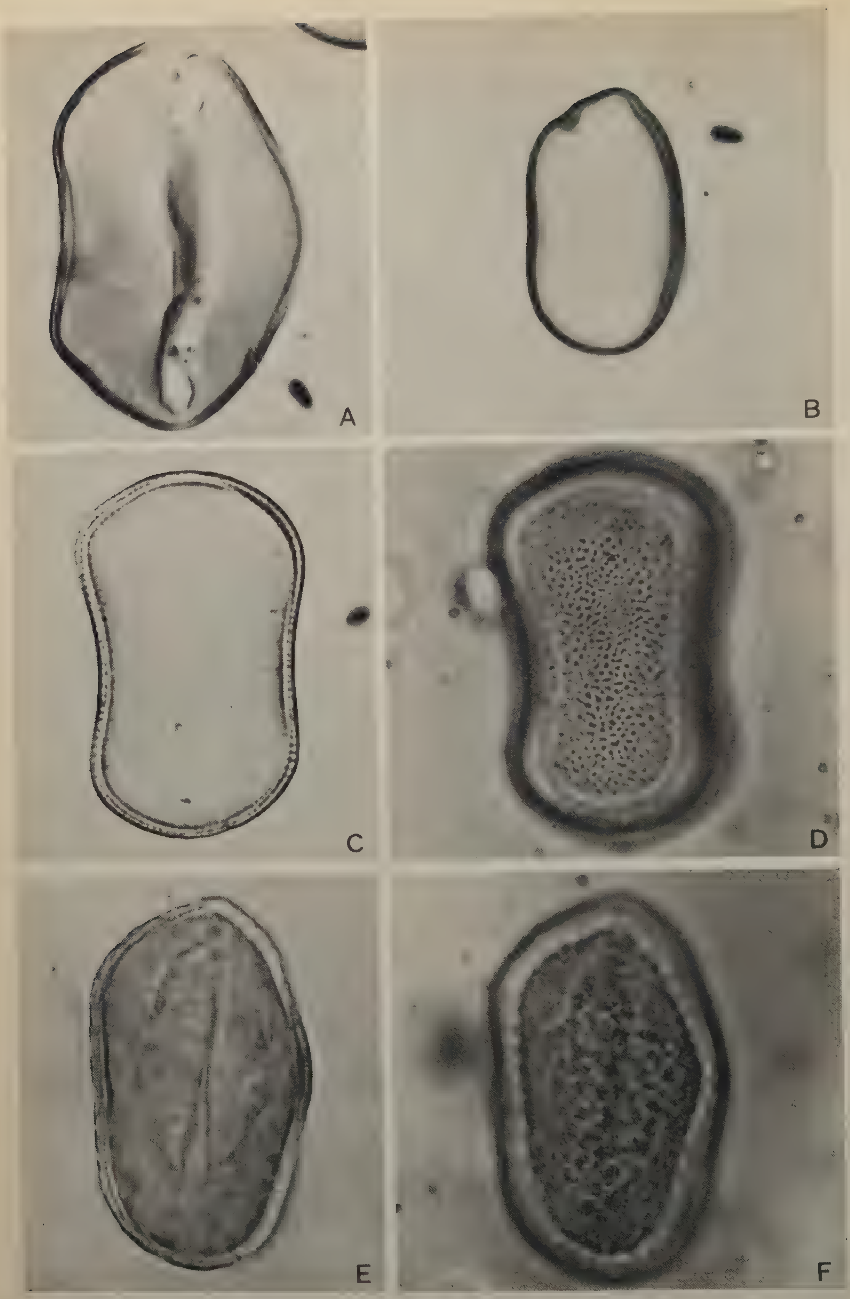
The genus *Kalbreyera* was founded on a single Kalbreyer collection and never found again. As the type specimen got lost during war-time at Berlin the genus could not be investigated in the present study.

The herbarium material used for this study was mostly obtained from the Utrecht Botanical Museum and Herbarium, and from sheets, which the second author has on loan from several other herbaria. The treatment of the pollen grains was according to the method described by Erdtman in 1960. Descriptions have been made with the aid of a Leitz Ortholux microscope, apochr., obj. × 63, × 90 and an eyepiece × 10. Photographs were made with the same microscope and lenses. The same terminology was used as in the previous study of palm pollen grains (Punt and Wessels Boer, 1966).



A. and B. *Calyptrogyne donnell-smithii*; A. surface pattern at proximal pole, B. optical section. C. *Calyptronoma clementis*; surface pattern at proximal pole. D. *Calyptronoma occidentalis*; surface pattern at proximal pole. E. *Taenianthera tamandua*; surface pattern at proximal pole. F. *Geonoma poiteauana*; surface pattern at proximal pole.

PLATE I



A. *Welfia georgii*; optical section. B. *Geonoma schottiana*; optical section. C. and D. *Astrogyne martiana*; C. optical section, D. surface pattern at proximal pole. E. and F. *Pholidostachys pulchra*; E. optical section, F. surface pattern at proximal pole.

Plate II

DESCRIPTION OF THE MATERIAL

In the Geonomoid palms the pollen grains do not have many distinctive characters. The grains are always monocolpate. In this respect they differ from the Cocoid palms, in which several species have a mixture of monocolpate and trichotomocolpate grains. The shape of the grains is usually slightly asymmetric, although there are some species having pollen grains which are nearly symmetric. Usually the longest axis of the grains, which follows the colpus, is distinctly larger than the diameter perpendicular on this axis. This diameter is largest when the pollen grains are observed from the distal or from the proximal view. In some pollen types (Calyptrogyne glauca type) the ratio between the two axes is nearly equal.

It is possible to group species into pollen types largely differentiated from one another on the basis of the exine characters. As was found in the Cocoid pollen grains the Geonomoid pollen grains show transitions from one type to another. The Geonoma type seems to be the basic type from which all other types can be derived. Several series of pollen variation can be constructed. One series can be made from small grains to large ones (e.g. *Geonoma schottiana* and allied forms → Welfia spec.). Another series is from thin exine without structure to thicker exine with distinct structure. This thickness is caused by the larger columellae and capita. Two types of structure can be distinguished:

1. Reticulate structure (Asterogyne type)
2. Vermiculate structure (Calyptronoma occidentalis type)

Geonoma type

Pollen grains monocolpate. Shape of the grains slightly irregular; the longest axis usually distinctly larger than the largest breadth. Sometimes the ratio between the axes is nearly equal. Grains usually between 30 and 40 μ. In *Welfia* the grains are larger.

Exine thin. Sexine (ektexine) thicker than nexine (endexine). Columellae usually indistinct. Most species have indistinct capita. Some species have capita which are more or less visible (*Geonoma stricta*, *G. piscicauda*).

To this type belong *Geonoma baculifera*, *G. deversa*, *G. interrupta*, *G. leptospadix*, *G. maxima*, *G. piscicauda*, *G. pohliana*, *G. schottiana*, *G. stricta*, *G. umbraculiformis*, *G. undata*, *Calyptronoma kalbreyeri*, *Calyptronoma synanthera*, *Welfia georgii*, and *W. regia*.
? *Geonoma poiteauana* and *Taenianthera tamandua*.

The Geonoma type is a type with rather indistinct characters. The pollen grains are rather small, the shape is slightly asymmetric with one usually noticeably longer axis and an exine without a distinct structure. In this basic type, however, some species are transitional in that they have certain characters typical of the types with a distinct ornamentation.

A. The *Welfia* species have pollen grains which are larger than those of the other species in the Geonoma type.
B. Some species have pollen with more distinct capita (e.g. *Geonoma*

deversa, G. piscicauda, Calyptronoma kalbreyeri). The pollen grains of *Geonoma stricta* have distinct capita and rather large columellae.
C. In *Geonoma umbraculiformis* the pollen grains have a rather thick exine (ca 2 μ) and the tectum is distinctly perforated. In this respect this species is transitional to *Geonoma poiteauana* and *Taenianthera tamandua* and also to the Calyptrogyne glauca type.
D. The pollen grains of *Geonoma poiteauana* and *Taenianthera tamandua* seem to be transitional to the Asterogyne type.

Asterogyne type

Pollen grains monocolpate. Shape only slightly asymmetric. Longest axis distinctly longer than the greatest breadth. Grains rather large; ca 45 μ. Exine rather thin. Sexine (ektexine) thicker than nexine (endexine). Grains finely, but distinctly reticulate. Columellae distinct. Lumina small; ca 1 μ, muri simplibaculate.

Asterogyne martiana, Taenianthera acaulis.
Geonoma poiteauana and *Taenianthera tamandua* are transitions to the Geonoma type.

The Asterogyne type can easily be recognised by its fine, but distinct reticulum. The muri (bacula) forming this reticulum are distinctly visible.

Geonoma poiteauana and *Taenianthera tamandua* have pollen grains which are very similar in most characters. However, the perforations in the *Taenianthera* species are larger than in the *Geonoma* species.

The pollen grains of these species are transitional between the Geonoma type and the Asterogyne type. The columellae are indistinct which character is in accordance with that in the Geonoma type. The distinct capita and large perforations in the tectum are characters which occur in the Asterogyne type. On the other hand the perforations are too small to call them a reticulum.

There is also a possibility that *Geonoma poiteauana* is a transition to the Calyptrogyne glauca type. The tectum perforatum is a character which occurs in this type too, but the shape of the grains is more in accordance with the Geonoma and Asterogyne types.

Calyptrogyne glauca type

Pollen grains monocolpate. Shape of the grains slightly asymmetric, more or less spheroidal. Longest axis slightly longer than the greatest breadth. Grains rather large; at least 40 μ. Exine thick. Sexine (ektexine) thicker than nexine (endexine). Tectum thick, slightly undulating. Perforations present in the tectum. These perforations inordinate arranged or sometimes in very short chains. Capita indistinct, columellae indistinct.

Calyptronoma clementis, Calyptronoma intermedia, Calyptrogyne donnell-smithii, Calyptrogyne glauca, Calyptrogyne trichostachys.

The type is characterised by the thick, slightly undulating tectum; by the inordinate arrangement of the perforations in the tectum and by its shape.

Calyptronoma occidentalis type

Pollen grains monocolpate. Longest axis larger than the greatest breadth. Grains rather large; at least 40 μ. Exine thick. Sexine (ektexine) thicker than nexine (endexine). Tectum thick, distinctly undulating. Perforations in the tectum arranged in chains. Ornamentation "vermiculate". Capita and columellae indistinct.

Calyptronoma occidentalis, *Calyptrogyne brachystachys*, *Pholidostachys pulchra*, *Aristeyera spicata.*

This type is characterised by its vermiculate ornamentation. Although *Pholidostachy spulchra* differs from the other three species in this type by the shape and largeness of the grains, the vermiculate ornamentation is so distinct, that it seems better to place the species in this type.

List of investigated species

Aristeyera spicata H. E. Moore — Tamayo 4177 (US)
Calyptronoma occidentalis type. Longest axis ca 50 μ. Exine ca 2,5 μ.

Asterogyne martiana (Wendl.) Wendl. [Plate II C, D] — Archer 1978 (US); Schipp 392 (K)
Asterogyne type. Longest axis ca 45 μ. Exine ca 2 μ. Lumina of the reticulum ca 1 μ.

Calyptrogyne brachystachys Wendl. ex Burret — Standley et Valerio 44775 (US)
Calyptronoma occidentalis type. Longest axis ca 55 μ. Exine ca 2,5 μ. Perforations rather few in short chains, nearly inordinate.

Calyptrogyne donnell-smithii (Dammer) Burret [Plate I A, B] — H. Johnson 1135 (US)
Calyptrogyne glauca type. Longest axis ca 60 μ. Exine ca 2,5 u.

Calyptrogyne glauca (Oerst.) Wendl. — Pittier 4305 (US)
Calyptrogyne glauca type. Longest axis ca 55 μ. Exine ca 2 μ.

Calyptrogyne trichostachys Burret — Stork $117^{1}/_{2}$ (US)
Calyptrogyne glauca type. Longest axis ca 60 μ. Exine ca 1,5 μ.

Calyptronoma clementis (León) A. D. Hawkes [Plate I C] — Wright 1466 (P)
Calyptrogyne glauca type. Longest axis ca 40 μ. Exine ca 2 μ.

Calyptronoma intermedia (Griseb. et Wendl.) Wendl. — Wright 3972 (P)
Calyptrogyne glauca type. Longest axis ca 40 μ. Exine ca 2 μ.

Calyptronoma kalbreyeri (Burret) Bailey — Killip et Smith 15314 (US)
Geonoma type. Longest axis ca 35 μ. Exine ca 1,5 μ. Capita distinct.

Calyptronoma occidentalis (Sw.) H. E. Moore [Plate I D] — Wessels Boer 1662 (U)
Calyptronoma occidentalis type. Longest axis ca 50 μ. Exine ca 3 μ.Perforations distinctly in chains.

Calyptronoma synanthera (Mart.) Bailey — Pavon s.n. (M)
Geonoma type. Longest axis ca 38 μ. Exine ca 1 μ.

Geonoma baculifera (Poiteau) Kunth — Wessels Boer 325 (U)
Geonoma type. Longest axis ca 35 μ. Exine ca 1 μ.

Geonoma deversa (Poiteau) Kunth — Wessels Boer 320 (U)
Geonoma type. Longest axis ca 30 μ. Exine 1–1,5 μ. Capita visible.

Geonoma interrupta (Ruiz et Pavon) Mart. — Wessels Boer 1635 (U)
Geonoma type. Longest axis ca 30 μ. Exine ca 1 μ.

Geonoma leptospadix Trail — Wessels Boer 912 (U)
Geonoma type. Pollen grains not quite mature.

Geonoma maxima (Poiteau) Kunth — Wessels Boer 1617 (U)
Geonoma type. Longest axis ca 30μ. Exine ca 1 μ

Geonoma piscicauda Dammer — Rombouts 880 a (U)

Geonoma type. Longest axis ca 45 μ. Exine ca 1,5 μ. Capita rather distinct.

Geonoma pohliana Mart. Reitz et Klein 2338 (HBR)

Geonoma type. Longest axis ca 35 μ. Exine 1–1,5 μ.

Geonoma poiteauana Kunth [Plate I F] Wessels Boer 1579 (U)

Asterogyne type. Longest axis ca 40 μ. Exine 1,5 μ. Rather thick tectum with distinct perforations, which are so large that it is a transition to a reticulum.

Geonoma schottiana Mart. [Plate II B] Reitz et Klein 9655 (HBR)
Foster 2503 (SPL)

Geonoma type. Longest axis ca 30 μ in Reitz et Klein specimen and 38 μ in the Foster specimen (Erdtman, 1952). Exine ca 1 μ.

Geonoma stricta (Poiteau) Kunth Wessels Boer 1558 (U)

Geonoma type. Longest axis ca 40 μ. Exine ca 1,5 μ. Capita and collumellae rather distinct.

Geonoma umbraculiformis Wessels Boer Versteeg 322 (U)

Geonoma type. Longest axis ca 40 μ. Exine thick; ca 2 μ. Capita distinct. Perforations in the tectum inordinate arranged. Transition to the pollen of *Geonoma poiteauana*.

Geonoma undata Klotzsch Linden s.n. (L)

Geonoma type. Longest axis ca 35 μ. Exine ca 1 μ.

Pholidostachys pulchra Wendl. ex Burret [Plate II E, F]
Standley et Valerio 48937 (US)

Calyptronoma occidentalis type. Longest axis ca 40 μ. Exine ca 1,5 μ.

Taenianthera acaulis (Mart.) Burret Ule 5594 (L)

Asterogyne type. Longest axis ca 45 μ. Exine 1,5–2 μ.

Taenianthera tamandua (Trail) Burret [Plate I E] Benoist 1708 (P)

Geonoma type or Asterogyne type. Longest axis ca 45 μ. Exine ca 1,5 μ. Perforations in tectum larger than in *Geonoma poiteauana*.

Transition between the Geonoma type and the Asterogyne type.

Welfia georgii Wendl. ex Burret [Plate II A] Wendland s.n. (K)

Geonoma type. Longest axis ca 45 μ. Exine ca 1,5 μ.

Welfia regia Wendl. Cuatrecasas 16932 (US)

Geonoma type. Longest axis ca 55 μ. Exine ca 1,5 μ.

Discussion

As may be clear from the introduction, it is hardly possible to detect any correlation with the floral characteristics. In this case pollen morphology proves to be of little help in classification. The flowers as well as the pollen grains of *Welfia* seem to be less advanced. The apparently highly specialized flowers of *Geonoma* have pollen of the same type but smaller.

Most remarkable is the situation in the genera *Calyptrogyne*, *Calyptronoma*, and *Pholidostachys*. These genera, all with the same type of flowers, have been separated on the structure of inflorescence and fruit. Here the pollen morphology of the species belonging to these genera proved to be rather heterogeneous. The pollen diversity, however, is in disagreement with the other characteristics. The pollen of *Calyptronoma occidentalis* and the hardly distinguishable *C. clementis* and *C. intermedia* belong to different types. Furthermore the very closely related *C. kalbreyeri* and *C. synanthera* differ much in their pollen types which are placed in the Geonoma type and the Calyptronoma occidentalis type respectively.

The same holds true for Calyptrogyne: *C. brachystachys* has pollen of the Calyptronoma occidentalis type; pollen of the other investigated species is referred to a Calyptrogyne glauca type.

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ÜBER EINIGE FOSSILE PALMENARTIGE HÖLZER AUS DEN ÖSTLICHEN NIEDERLANDEN

J. VAN DER BURGH UND J. E. MEULENKAMP

(*Bot. Museum und Herbarium, Utrecht und Geologisches Institut, Utrecht*)

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ABSTRACT

A study was made of the structure of 32 fossil palmlike wood samples, found in diluvial sands in the East of the Netherlands. 27 of them proved to belong to four species of *Palmoxylon*; two of them are described as new. Five samples belong to a palmroot structure newly described here.

EINLEITUNG

Als im Jahre 1904 STENZEL seine grosse Arbeit über fossile Palmenhölzer veröffentlichte, beschrieb er darin ein Stück Palmenholz aus den Niederlanden als *Palmoxylon porosum*. Seitdem sind viele sogen. Palmenhölzer in der Umgebung von Eibergen und Vragender gesammelt worden. Es erhob sich die Frage, ob alle diese Hölzer zu *Palmoxylon porosum* gehören, oder ob sie mehrere Arten darstellen. Die vorliegende Arbeit enthält die Ergebnisse einer Untersuchung von 32 Stücken, wovon 22 zu *P. porosum* Stenzel gehörten.

MATERIAL UND METHODIK

Die meisten Stücke befinden sich in Privatsammlungen. An dieser Stelle möchten wir den Herren de Graaf, Jansen, Koenderink, Kolstee, Kortenbout van der Sluys, Rhebergen und Stam, die uns ihr Material zur Verfügung stellten recht herzlich danken. Ausserdem verdanken wir noch den Sammlungen des Reichsmuseums für Mineralogie etc, zu Leiden, des Museums Natura Docet zu Denekamp und des Naturhistorischen Museums zu Enschede einige wertvolle Stücke. Die Arbeit wurde ausgeführt im Institut für systematische Botanik der Reichsuniversität Utrecht (Direktor Herr Prof. J. Lanjouw), Abteilung Paläobotanik und Pollenmorphologie (Leitung Herr Prof. F. P. Jonker). Wir danken Herr RODING (1956) für seine Hilfe bei dem Auffinden des Materials und das stätige Interesse mit dem er unsere Arbeit begleitet hat. Wir danken weiter Herrn H. A. Elsendoorn für die schnelle Herstellung der benötigten Dünnschliffe und Herrn Frank de Vries für seine unschätzbare Hilfe bei der Mikrofotografie. Ebenfalls danken wir Herrn Dr. K. U. Kramer für das kritische Durchlesen des Manuskriptes.

Von sämmtlichen verkieselten Stücken, die als Diluvialgeschiebe in sandigen Ablagerungen gefunden worden waren, wurden Dünnschliffe angefertigt. Von jedem Stück wurde mindestens ein Querschnitt und wenn nötig, ein Längsschnitt hergestellt. Die verschiedenen Formen wurden zum Bestimmen mit rezenten und fossilen Hölzern verglichen, und zwar mit Dünnschnitten und Beschreibungen. Die Dünnschliffe sind der Sammlung des Instituts für systematische Botanik der Reichsuniversität Utrecht einverleibt worden.

Die Mikrofotografien wurden mit einem Leitz-Ortholux-Mikroskop und mit einer Orthomat-Kamera aufgenommen.

Für die Nomenklatur wurde die klassische Methode, die der Formgattungen und -arten, beibehalten. Besonders bei "Palmenhölzern" ist grosse Vorsicht geboten, denn viele Monokotyledonen besitzen einen ähnlichen Bau. Dies wurde aufs neue von WEYLAND und KILPPER (1964) unter Beweis gestellt. Sie konnten zeigen, dass *Palmoxylon bacillare* mindestens teilweise nicht von einer Palme, sondern von einer Bromeliazee stammt.

ERGEBNISSE

Es fanden sich folgende Hölzer:

ANGIOSPERMAE
MONOCOTYLEDONAE

Palmoxylon Schenk 1882

Palmoyglon porosum Stenzel 1904 **(Tafel I)**

BESCHREIBUNG DES HOLZES

Dermale Zone: Faserbündel zahlreich, ziemlich dicht beisammen stehend. Das parenchymatische Grundgewebe ist aus isodiametrischen oder etwas gestreckten Zellen zusammengesetzt. Die Interzellularen sind ebenso gross wie die umringenden Zellen und voneinander durch eine etwa vier Zellen dicke Parenchymschicht getrennt. Die Grenze zu der folgenden Zone ist ziemlich scharf.

Subdermale Zone: Hier fehlen die Faserbündel vollkommen. Die Faserleitbündel sind einander bis auf die Hälfte ihrer Breite genähert; ihre Faserteile sind ebenso gross wie die Leitbündelteile oder etwas grösser. Die Faserbelege sind sehr dickwandig. Das parenchymatische Grundgewebe ist aus isodiametrischen oder etwas gestreckten Zellen zusammengesetzt, ebenso wie in der dermalen Zone. Auch hier sind die Interzellularen nur spärlich, aber regelmässig verteilt. Ihre Entfernung ist mehrere Parenchymzellenschichten gross; ihre Grösse ist ungefähr gleich der einer Parenchymzelle.

Zentrale Zone: In der Mitte des Stammes befindet sich die zentrale Zone, welche nach aussen allmählich in die subdermale Zone übergeht. Die Faserleitbündel stehen weiter von einander entfernt, bis zu 2–6 × ihre Breite. Die Faserteile sind ebenso wie in der subdermalen Zone, sehr dickwandig, aber ihr Umfang ist kleiner als der der Leitbündelteile. Die Leitbündelteile zeigen meist 2, nur vereinzelt 1, 3 oder 4 grosse Gefässe und eine kleine Anzahl von schmalen Elementen. Immer ist das Grundgewebe strahlig um die Faserleitbündel angeordnet. Das Grundgewebe ist ganz locker, die Interzellularen sind von einander durch eine nur eine oder (seltener) zwei Zellen starke Parenchymschicht getrennt; die Parenchymzellen sind nicht isodiametrisch, sondern gestreckt, und mit Ausstülpungen versehen. In diesem Holz sind die Faserbelege der Faserleitbündel meistens durch röhrenförmige Löcher vertreten. Nach diesem Merkmal hat Stenzel die Art benannt. Er hat sie u.a. auf Grund hiervon dem *P. germanicum* gegenübergestellt, bei dem nicht der Faserteil, sondern der Leitbündelteil des Faserleitbündels zuerst zerstört wird. Das

Verschwinden gewisser Gewebeteile ist aber ein Erhaltungszustand. Bei *Palmoxylon bacillare* aus der Braunkohle ist der Leitbündelteil zuerst vermodert (VAN DER BURGH, 1964). *P. germanicum* ist ein verkieselter Stamm (CONWENTZ, 1882), ebenso wie dieses und die nachfolgenden Hölzer, von denen auch nur eines ganz vereinzelt ein gutes Leitbündel zeigt. Ferner gibt es unter den untersuchten Stücken solche, bei denen der Faserteil ziemlich gut oder sehr gut erhalten ist, und andere, bei denen man alle Übergänge von gutem zu schlechtem Erhaltungszustand finden kann. Dieses gilt nicht nur für *P. porosum*, sondern auch für die drei anderen Arten.

WURZELN

Im Grundgewebe verschiedener Stücke finden sich in der subdermalen Zone auch Wurzeln. Es sind zweifellos Wurzeln mit Palmenwurzelbau: ein kleiner zentraler Zylinder mit zentralem Xylem, einem Ring von Phloem, einer deutlichen Endodermis und einer dicken Rinde, in der an einer Stelle ein Kranz von Kanälen, wie diese bei den Palmen öfters beobachtet werden, zu finden ist.

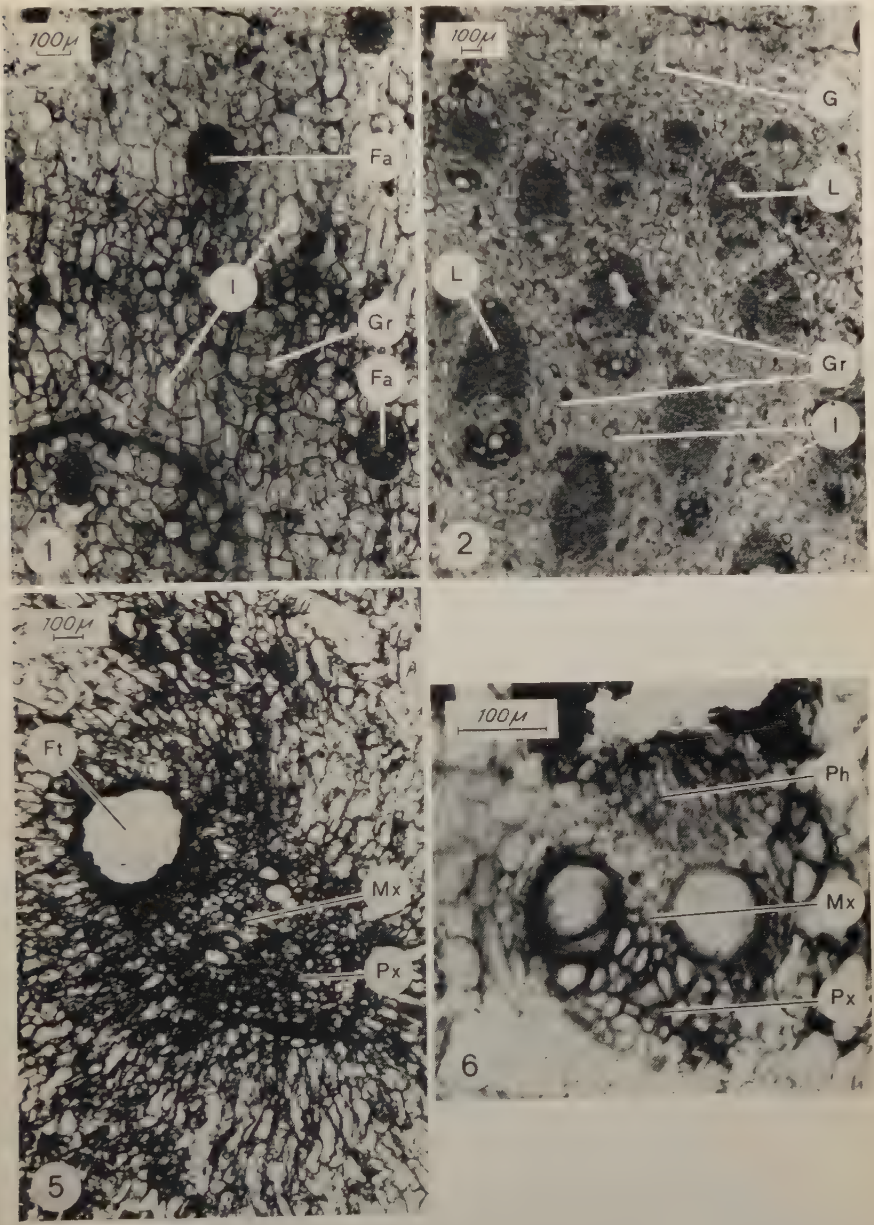
Im übrigen gleichen diese Wurzeln sehr den von STOCKMANS et WILLIÈRE (1943) als *Palmoxylon sp.* (Seite 61) beschriebenen Resten. Beim Vergleichen dieses Holzes mit den Beschreibungen schon bekannter Palmoxylonarten können nur die Arten in betracht gezogen werden, die durch das Vorkommen eines lockeren Grundgewebes und das Fehlen der Faserbündel charakterisiert sind. Von diesen schalten die Formen mit nicht strahlig um die Faserleitbündel angeordnetem Grundgewebe aus. Es bleiben nur noch 6 Arten übrig; *Palmoxylon porosum*, *P. cellulosum*, *P. blanfordii*, *P. remotum*, *P. fladungii* und *P. rutotii*. Von den letzten fünf dieser Hölzer sind in den Faserleitbündeln die Verhältnisse in der Grösse zwischen Faserteil und Leitbündelteil anders als bei diesem Holz. Nur *P. porosum* ist recht ähnlich gebaut, und aus diesem Grunde wird unser Material hier zu dieser Art gestellt.

Palmoxylon pachyoxylon van der Burgh et Meulenkamp **(Tafel II)**

BESCHREIBUNG DES HOLZES

Die Faserleitbündel stehen im Querschnitt regelmässig zerstreut. Ihre Entfernung schwankt zwischen etwa ihrer eigenen Breite in der zentralen Zone und der Hälfte ihrer Breite in der subdermalen Zone. Die Form ist im Querschnitt länglich-rund, der Faserteil ist 2–3 Mal so gross wie der Leitbündelteil. Im Leitbündel findet man meistens 2, zuweilen aber auch 3 oder 4 grosse Gefässe. Das mediane Xylem ist ziemlich gross, ebenso das dickwandige Phloem. Das Leitbündel ist meistens gut erhalten, während der Faserteil oft ganz oder zum Teil geschwunden und teilweise durch Chalzedon ersetzt ist. Die Sklerenchymfasern sind dickwandig, der Faserteil umfasst drei Viertel des Umfanges des Leitbündelteils. Zuweilen findet sich ein zweiter, schmälerer Faserteil gegenüber dem Ersten am Leitbündelteil. Dieser Letztere ist dann amphiphloisch.

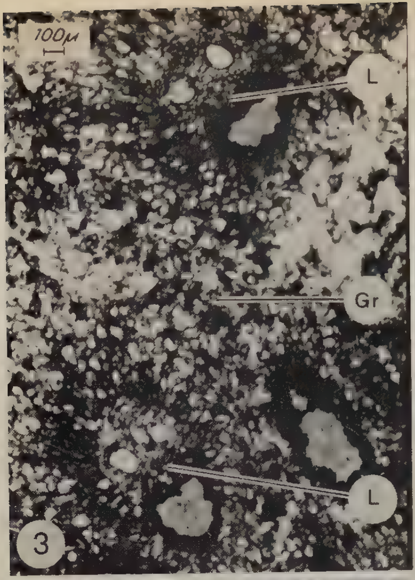
Faserbündel fehlen in diesem Holz.

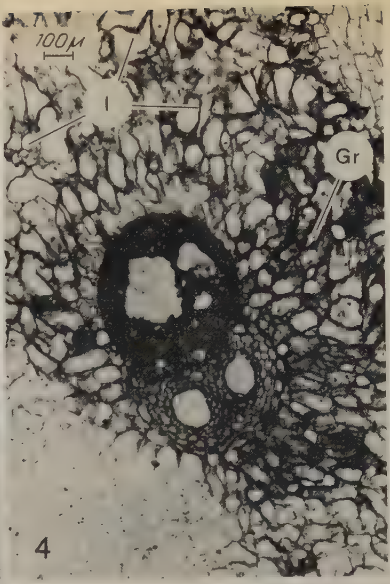


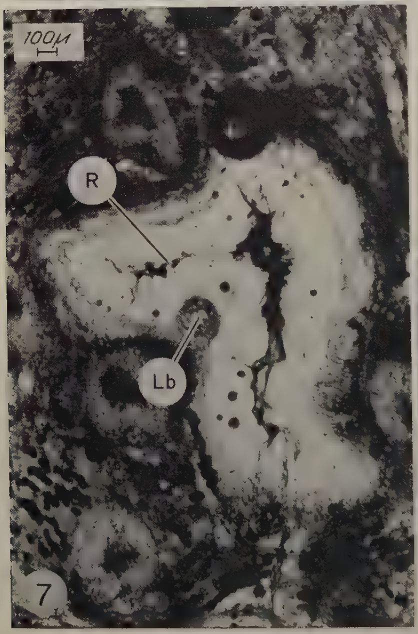
Palmoxylon porosum Stenzel
Fig. 1. Übersicht der dermalen Zone; Fig. 2. Übersicht der subdermalen Zone; Fig. 3. Übersicht der zentralen Zone; Fig. 4. Faserleitbündel aus der Übergang zwischen zentralen und subdermalen Zone.

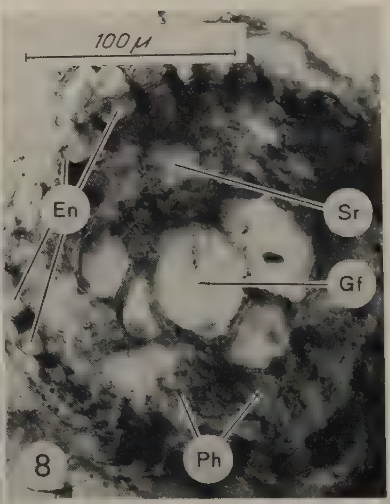
TAFEL IA

Facing p. 278



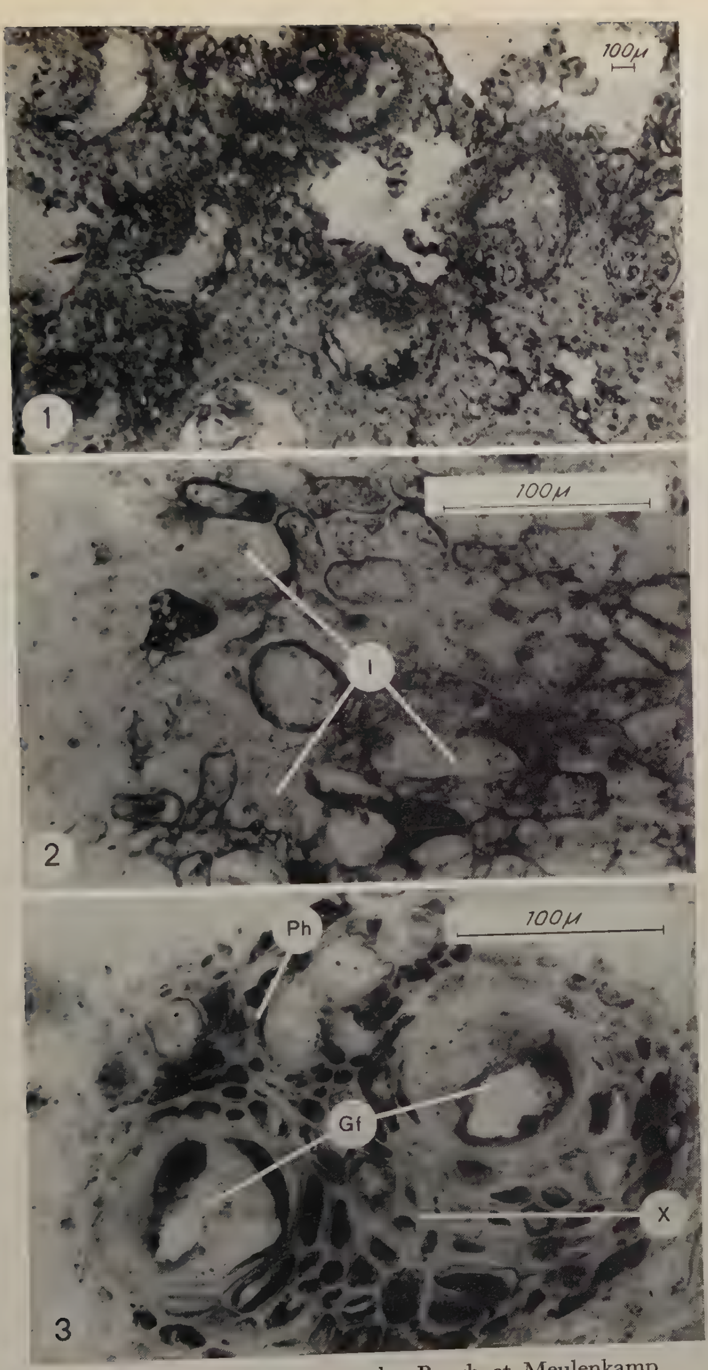






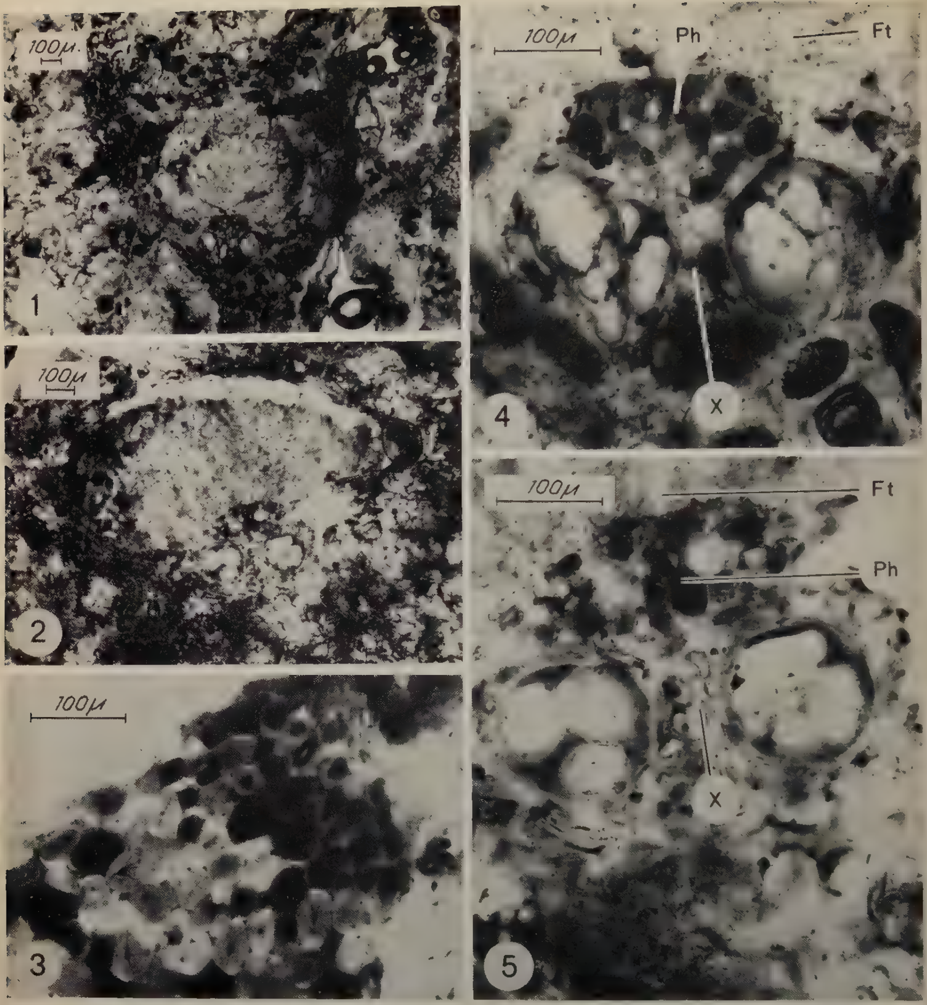
Palmoxylon porosum Stenzel (*Fortsetzung*)
Fig. 5. Faserleitbündel aus der zentralen Zone; Fig. 6. Leitbündelteil eines Faserleitbündels; Fig. 7. Übersicht der subdermalen Zone mit einem Wurzelspur; Fig. 8. Leitbündel der Wurzel aus Fig. 7.

TAFEL IB



Palmoxylon pachyoxylon van der Burgh et Meulenkamp
Fig. 1. Übersicht; Fig. 2. Grundgewebe; Fig. 3. Leitbündelteil des Faserleitbündels.

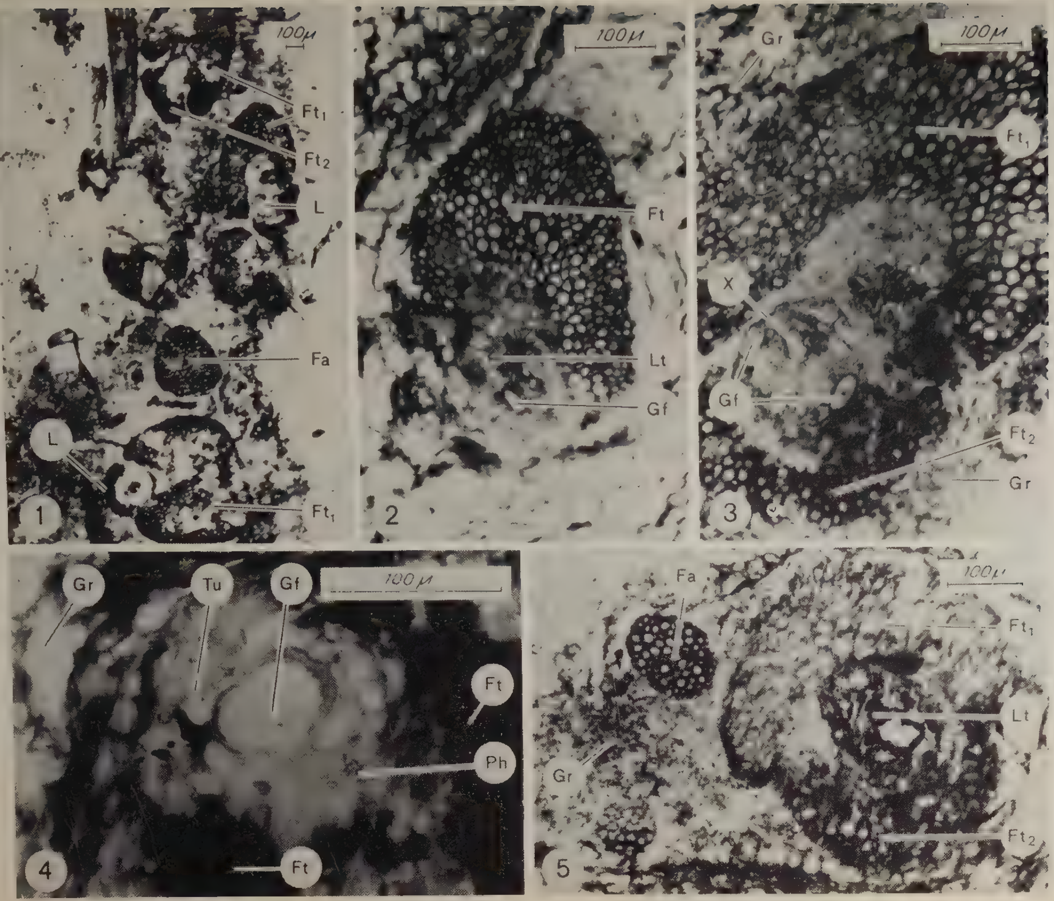
TAFEL II



Palmoxylon variabile Vater
Fig. 1. Faserleitbündel im Grundgewebe; Fig. 2. Faserleitbündel; Fig. 3. Faserteil eines Faserleitbündels; Fig. 4. Leitbündelteil des Bündels aus Fig. 1; Fig. 5. Leitbündelteil des Bündels aus Fig. 2.

TAFEL III

TAFEL IV



Palmoxylon eibergense van der Burgh et Meulenkamp (Figs. 1, 2, 3, 5: Typus; Fig. 4: Stück aus Zwilbroek)

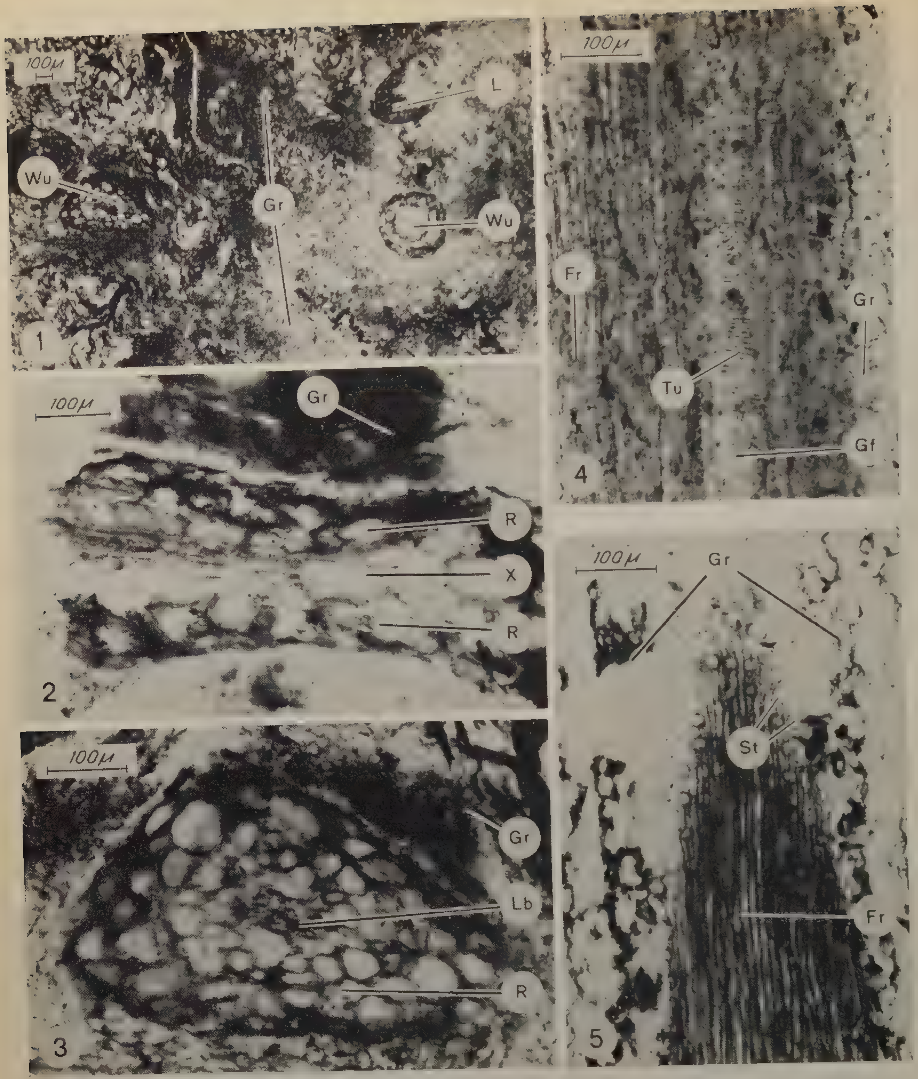
Fig. 1. Übersicht;

Fig. 2. Übergang zwischen Faserbündel und Faserleitbündel;

Fig. 3. Grosser Faserleitbündel;

Fig. 4. schmaler Leitbündelteil, die Tracheiden schiefgeschnitten;

Fig. 5. Faserleitbündel mit vermodertem Leitbündelteil.

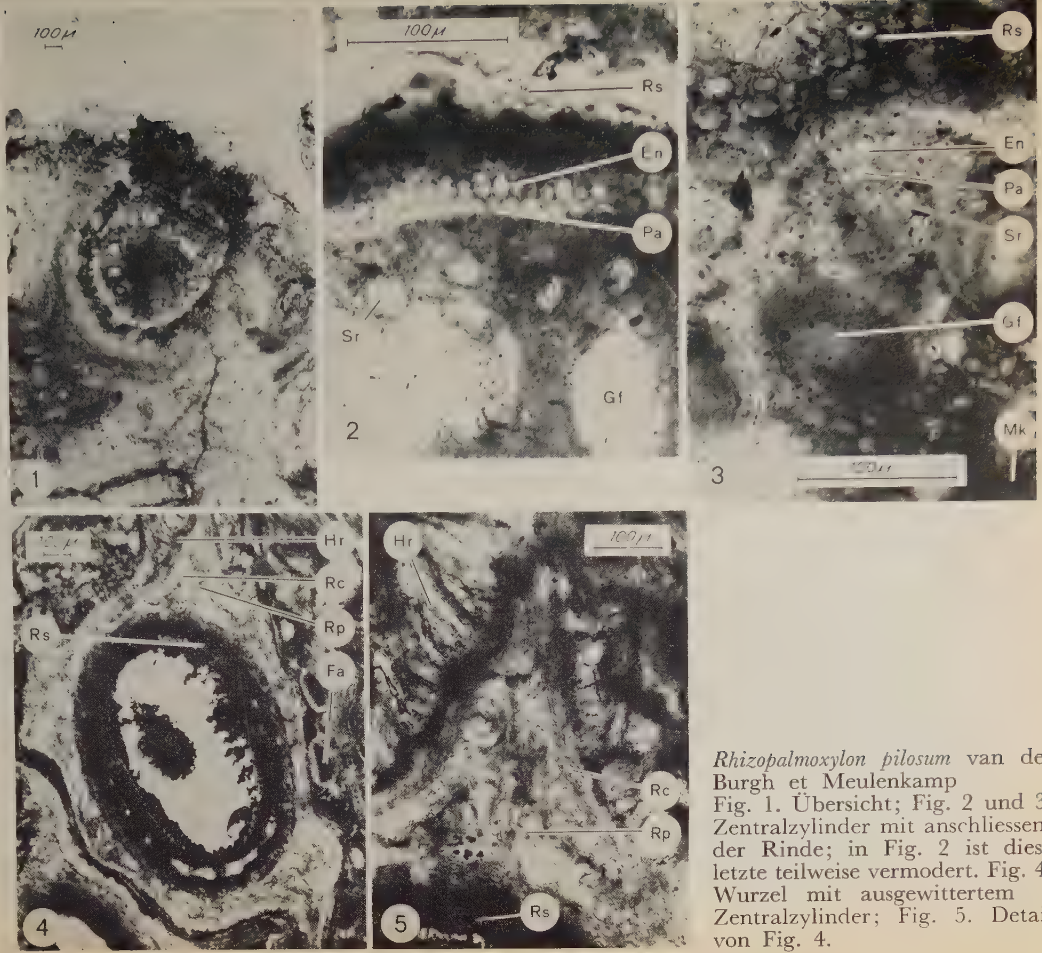


Palmoxylon eibergense van der Burgh et Meulenkamp (Figs. 1–4: Typus; Fig. 5: Stück aus Zwilbroek)

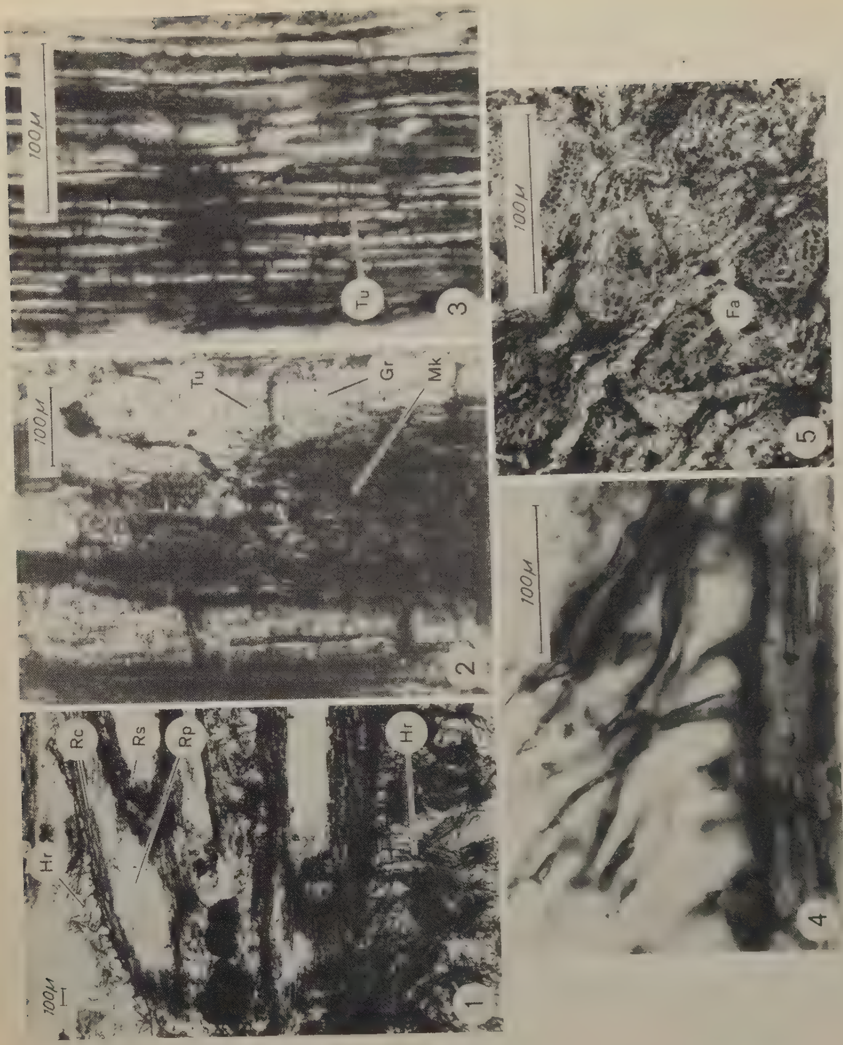
Fig. 1. Übersicht mit Wurzeln; Fig. 2. Längsschnitt einer Wurzel; Fig. 3. Wurzelquerschnitt; Fig. 4. Längsschnitt eines Faserleitbündels; Fig. 5. Längsschnitt des Faserteils eines Faserleitbündes.

TAFEL V

TAFEL VI



Rhizopalmoxylon pilosum van der Burgh et Meulenkamp
Fig. 1. Übersicht; Fig. 2 und 3. Zentralzylinder mit anschliessender Rinde; in Fig. 2 ist diese letzte teilweise vermodert. Fig. 4. Wurzel mit ausgewittertem Zentralzylinder; Fig. 5. Detail von Fig. 4.



Rhizopalmoxylon pilosum van der Burgh et Meulenkamp
Fig 1. Übersicht einer Längsschnitt; Fig. 2. Längsschnitt eines Zentralzylinders; Fig. 3. Längsschnitt der Sklerenchymatischen Rinde; Fig. 4. Haare; Fig. 5. Reste der Stammrinde (Cortex).

TAFEL VII

Das Grundgewebe ist locker, mit vielen grossen Interzellularen und parenchymatischen, unregelmässig geformten Zellen. Um die Faserleitbündel bildet das Grundgewebe eine bis zu 2 oder 3 Zellen starke Schicht; darauf folgt das lockere Parenchym mit den vielen Interzellularen. Diese Parenchymzellen stehen strahlig rundum die Faserleitbündel angeordnet, doch ist das nicht besonders ausgeprägt. Im Längsschnitt fällt sogleich der grosse Holzteil auf, dessen Treppentüpfel schön konserviert sind. An die Faserbelegen sind viele Stegmata ausgebildet.

Von dieser Art lag nur ein Stück vor: ein kleines Stück aus der Sammlung des Reichsmuseums für Mineralogie etc. zu Leiden (Nr 62321), dies ist zugleich der Typus. Als Fundort wird Sibculo angegeben. Schon am ganzen Stück kann man sehen, dass die Faserleitbündel schmäler sind und mehr gedrängt stehen als bei der vorigen Art. Es stammt aus der subdermalen und zentralen Schicht eines Stammes.

Im Bau des Faserteils der Faserleitbündel unterscheidet sich dieser Art sofort von *P. porosum*. Auch der Bau der Leitbündel ist anders. Vergleicht man dieses Holz mit Palmenhölzern ohne Faserbündel und mit lockerem Parenchym, so ergibt sich, dass keine der oben bei *P. porosum* genannten Arten mit diesem Holz in genügend Einzelheiten übereinstimmt um auf Zusammengehörigkeit schliessen zu können. Auch *P. paniselianum* hat abweichende Merkmale. Besonders das Grundgewebe ist verschieden (STOCKMANS et WILLIÈRE, 1943). Es handelt sich hier um eine neue Art, die nach dem verhältnismässig starken Holzgewebe *Palmoxylon pachyoxylon* genannt wird. Die Beschreibung soll als Diagnose gelten.

Palmoxylon variabile Vater 1884 **(Tafel III)**

BESCHREIBUNG DES HOLZES

Die Faserleitbündel sind breit, ihr Faserteil ist um ein Mehrfaches grösser als ihr Leitbündelteil, der von dem Faserteil nur wenig oder gar nicht umfasst wird. Die Fasern sind sehr starkwandig. Das Leitbündel enthält ein medianes kleines Protoxylem und einige Metaxylemelemente. Zu beiden Seiten steht meist nur ein grosses Gefäss. An der Sklerenchymkappe findet man einen Phloemstrang mit dünnwandigen Elementen. Auch hier ist in der Regel der Leitbündelteil besser erhalten als der Faserteil. Faserbündel fehlen. Das Grundgewebe ist parenchymatisch, dicht und aus ziemlich regelmässigen Zellen gebildet.

Auch von dieser Art liegt nur ein Stück vor. Es ist ein schmales, brettförmiges Stück, dass auf Grund der teilweise dicht gedrängten Stellung der Faserleitbündel und ihrer mehr oder weniger deutlichen Orientierung wohl der subdermalen Zone angehört. Als Fundort wird Westerhaar angegeben. Es stammt aus die Sammlung von Herrn Rhebergen zu Schonebeek. Von den Palmenhölzern mit dichtem Grundgewebe und ohne Faserbündel gleicht unser Holz den Beschreibungen und Abbildungen von *P. germanicum*, *P. loppemense* und

P. variabile am meisten. *P. loppemense* hat aber viel strahlig angeordnetes Grundgewebe, *P. germanicum* ein dichtes, aus isodiametrischen Zellen zusammengesetztes Grundgewebe mit nur kleinen Interzellularen, aber auch hier sind die Grundgewebezellen um die Übergangsbündel herum strahlig angeordnet, was bei unserem Stück nicht der Fall ist. *P. variabile* dagegen zeigt nur etwas verlängerte, den Faserbündeln anliegende Grundgewebezellen. Andere Punkte der Übereinstimmung sind: der gegenseitige Abstand der Faserleitbündel (schwankend von weniger bis etwas mehr als ihr Durchmesser), ihre sehr mannigfaltige Form, und der Faserteil, der an Grösse den Leitbündelteil stets übertrifft und auch in der Form ganz mit den Beschreibungen und Abbildungen von VATER (1884) und STENZEL (1904) übereinstimmt. Aus diesem Grunde wird unser Holz zu *Palmoxylon variabile* gestellt.

Palmoxylon eibergense van der Burgh et Meulenkamp (**Tafel IV, V**)

BESCHREIBUNG DES HOLZES

Die Bündel zeigen sich schon am Stück recht verschieden von denen der vorigen Arten, indem sie stark wellig verlaufen. Im parenchymatischen Grundgewebe, das aus isodiametrischen oder etwas gestreckten Zellen zusammengesetzt ist, findet man sowohl Faserbündel als auch Faserleitbündel. Ausserdem gibt es alle möglichen Übergänge zwischen beiden Formen von Bündeln. Schliesslich finden sich ziemlich viele Wurzelreste. Die Faserleitbündel stehen in allen Zonen des Zentralzylinders gleich dicht gedrängt. Im Inneren des Stammes zeigen sie keine Orientierung. Die Faserbelege sind dünnwandig und ziemlich oft zweiteilig, d.h. es ist ein grosses Faserbündel vorhanden, wie bei fast allen Palmoxyla, und ein zweites, kleineres am gegenüberliegenden Teil des Leitbündels. Oft sind beide Faserbündelteile verbunden und umschliessen zusammen den ganzen Leitbündelteil. Der Leitbündelteil enthält 1–5 ziemlich enge Gefässe. Die Übergänge zum Faserbündel werden gebildet durch Bündel mit einem verhältnismässig grossen Faserteil und einem kleinen oder sogar ganz winzigen Leitbündelteil.

WURZELN

Neben den Faserleitbündeln und Faserbündeln finden sich in allen Stücken dieser Art noch Wurzeln, deren Erhältungszustand mit dem des Faserleitbündels vergleichbar ist. Sie zeigen den gewöhnlichen Bau: dicke Rinde, bis zu 4 Zellen dick, also weniger als die der bisher beschriebenen Palmenwurzel, und nicht in sklerenchymatische und parenchymatische Gewebeschichten differenziert, sondern rein Parenchymatisch, also verschieden von den uns bekannten Palmenwurzeln. Der Zentralzylinder ist ausserordentlich schmal und umfasst nur wenige Xylem- und Phloemelemente.

Von dieser Art liegen drei Stücke vor: ein Stück aus Zwolle bei Groenlo (Sammlung Stam) ein zweites und ein drittes aus Zwilbroek bei Eibergen (Sammlungen Koenderink, Bilthoven und Naturhistorisches Museum, Enschede). Das erste Stück stammt aus der subdermalen und zentralen Zone des Stammes, das zweite hochstwahrscheinlich nur aus der subdermalen Zone, und das dritte ist zu klein, als dass mit genügender Sicherkeit etwas darüber ausgesagt werden könnte. Als Typus wird das Stück aus Zwolle bei Groenlo gewählt. Es gibt viele Palmenhölzer mit dichtem Grundgewebe und Faserbündeln neben den Faserleitbündeln. Von allen diesen gibt es aber nur wenige mit doppelten Faserbündeln an den Faserleitbündeln: *P. parvifasciculosum*, *P. scleroticum*, *P. hillebrandtii*, *P. wentii* und *P. pietzschii*. Keine dieser Arten stimmt aber völlig mit unserem Holz überein, denn bei *P. parvifasciculosum* ist der Faserteil schmaler als der Leitbündelteil, während bei unserem Holz die Verhältnisse gerade umgekehrt sind. Bei *P. scleroticum* sind die Grundgewebezellen angeblich zum Teil verholzt (VATER, 1884) was bei unserem Holz nicht der Fall ist. Auch sind dort, ebenso wie bei *P. wentii*, *P. hillebrandtii* und *P. pietzschii*, die Sklerenchymfasern stark verdickt (STOCKMANS et WILLIÈRE, 1943; Pax und Gingelsheim in PAX, 1907; SCHÖNFELD, 1955). Bei unserer Holzprobe dagegen sind sie verhältnismässig dünnwandig. Beim Durchsehen der Literatur stiessen wir auf die Beschreibungen von *P. bacillare* bei JURASKY (1930) und bei VAN DER BURGH (1964) und von *Bromeliaceophyllum rhenanum* bei WEYLAND und KILPPER (1964). Besonders mit der Beschreibung und den Figuren der letzteren Autoren besteht gute Übereinstimmung. Es finden sich in beiden Hölzern Übergänge zwischen Faserbündeln und Faserleitbündeln, eine gleichmässige Verteilung der Bündel über den ganzen Stammdurchschnitt, und nicht immer stark sklerotisierte Sklerenchymkappen. Hinzu kommt noch der abweichende Bau der Wurzeln. Aus diesem Grunde liegt es nahe, das Holz systematisch in der Nähe von *Bromeliaceophyllum rhenanum* zu stellen. Es bestehen auch gewisse Unterschiede zwischen unserem Holz und *Bromeliaceophyllum rhenanum*: eine Zweiteilige Sklerenchymkappe findet sich nur in unserem Holz, und *Bromeliaceophyllum rhenanum* zeigt in den äusseren Schichten stark verdickte Sklerenchymfasern, während bei unserem Holz alle Sklerenchymfasern gleich stark sind.

Über die Pflanze, zu der dieser Stamm gehört, wissen wir gar nichts, und es erscheint darum angebracht, das Holz in die Gattung *Palmoxylon* unter dem Namen *Palmoxylon eibergense* einzureihen. Als Diagnose soll die Beschreibung gelten.

Rhizopalmoxylon Gothan 1942.

Rhizopalmoxylon pilosum van der Burgh et Meulenkamp **(Tafel VI, VII)**

BESCHREIBUNG DES HOLZES

Dieses "Holz" ist aus zahlreichen Wurzeln, die mit einander verflochten sind, zusammengesetzt. Ausserdem finden sich noch Reste der dermalen Zone eines Palmenstammes.

Im Innern einer Wurzel befindet sich in der Mitte das sklerenchymatische Mark, ringsum vom Xylem umschlossen. Darauf folgt ein Ring von Phloem, nach aussen abgeschlossen von einer nur eine

Zelle starken Parenchymschicht. Der zentrale Zylinder wird nach aussen begrenzt von einer Endodermis, die etwas starkwandiger ist als die Phloem- und Parenchymschichten. Es folgt dann die Rinde, welche sehr dick ist. Sie ist von innen nach aussen folgendermassen strukturiert: zuerst sklerenchymatisch, dann parenchymatisch, und zuletzt kollenchymatisch. Die Epidermis trägt viele haarähnliche Papillen.

Oft ist der Zentralzylinder ausgewittert. In der sklerenchymatischen Rinde ist die Mittelpartie vermodert und nicht durch Quarz ersetzt worden, und der runde Zentralzylinder fällt als kleines Stäbchen heraus. Zwischen den Wurzel findet man vereinzelt kleine Gruppen von Stammrindengewebe, deren Grundgewebe ganz zerdrückt ist. Die Wurzelrinde wirft oft sehr starke Falten. Im Längsschnitt kann man die Treppentüpfel der Holzgefässe beobachten. Auch ist der Bau der Rinde im Längsschnitt oft besser zu unterscheiden. Die Sklerenchymatische innere Kortex zeigt sehr schöne Tüpfel, genau wie sie z.B. auch bei *Hyospathe elegans* wahrzunehmen sind.

Das Material kann aus Grund des palmenwurzelähnlichen Baues zu *Rhizopalmoxylon* GOTHAN (1942) gestellt werden. Wegen des verschiedenen Baues des zentralen Zylinders (nur ein Ring von Gefässen) wird es hier als einer neuen Art beschrieben unter dem Namen *Rhizopalmoxylon pilosum.*

Der Artnahme wurde gewählt auf Grund der vielen Epidermispapillen, die wie Haare aussehen und die Wurzeln ganz dicht verflechten.

Als Diagnose soll die Beschreibung gelten.

Von dieser Art liegen 5 Stücke vor. Vier davon sind so stark gebleicht und waren vor dem eintreten der Verkieselung auch so stark vermodert, dass nicht viel Struktur daran zu beobachten ist. Das Fünfte war besser erhalten und gestattete die mikroskopischen Strukturen zu untersuchen. Dieses letztes Stück wurde zum Typus gewählt und stammt aus der Sammlung von Herrn de Graaf, Arnhem, Fundort Rosendaal. Die vier andere Stücke stammen aus der Umgebung von Borne und Almelo.

ZUSAMMENFASSUNG

Es wurden insgesamt 32 Geschiebehölzer palmenartiger Natur aus den östlichen Niederlanden (Provinzen Gelderland und Overijssel) bearbeitet. Es stellte sich heraus, dass 27 Stücke zu 4 *Palmoxylon*-Arten gehören, darunter 2 neue; 5 Stücke gehören zu einer neu beschriebenen Palmenwurzelstruktur.

ERKLÄRUNG DER BUCHSTABEN IN DEN FIGUREN

En: Endodermis
Fa: Faserbündel
Fr: Faser
Ft: Faserteil
G: Grenze der dermalen Zone
Gf: Gefäss
Gr: Grundgewebe
Hr: Haare
I: Interzellular
L: Faserleitbündel
Lb: Leitbündel
Lt: Leitbündelteil des Faserleitbündels
Mk: Mark
Mx: Metaxylem
Pa: Parenchym
Ph: Phloem
Px: Protoxylem
R: Rinde
Rc: kollenchymatische Rinde
Rp: parenchymatische Rinde

Rs: sklerenchymatische Rinde
Sr: Siebrohr
St: Stegmata
Tu: Tüpfel
X: Xylem
Wu: Wurzel

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PALAEOBOTANY OF THE MESOPHYTIC II

NEW AND NOTEWORTHY JURASSIC FERNS FROM YORKSHIRE

JOHANNA H. A. VAN CITTERT

(*Botanical Museum and Herbarium, Division of Palaeobotany, Utrecht*)

(*received February 4th, 1966*)

Cladophlebis harrisii sp.n. Plate I, fig. A, B, C; text-fig. 1

DIAGNOSIS: Frond at least bipinnate. Rachis up to 2 mm broad, longitudinally grooved. Pinnae alternate or subopposite, up to 1,5 cm broad (normally 1 cm), longest one 5 cm long but without apex. Pinnae arising at intervals of 1–2,5 cm, and at an angle of 30–60°. Pinna-rachis thin. Pinnules arising at an angle of 45° at intervals of 1–6 mm, alternate, katadromic. Pinnules always united basally. Pinnules in the lower (or middle) part of the leaf linear, up to 1,5 cm long (normally 1 cm) and up to 4 mm broad (normally 2 mm). Apex obtuse, margin entire, slightly narrowed near the base, basal margin decurrent as a narrow wing along the pinna-rachis. In the upper part of the leaf pinnules smaller, 4 mm broad, 6 mm long, deltoid and slightly falcate. Proximally the pinnae are pinnulate, the pinnules becoming first laterally fused and then forming an entire pinna.

Venation: Midrib arising at a small angle near the basal edge of the pinnule and bending outwards or, sometimes, straight to the apex. Lateral veins arising in katadromic order or nearly opposite, at intervals of 1–2 mm and at an angle of 40°, simple or once forked half-way towards the margin; branches diverging.

Substance of lamina fairly thick, margins flat.

No fertile material found until now.

DISTRIBUTION: Most of the material is from Hasty Bank, but there are some specimens from Esklets Cragg, Westerdale and Roseberry Topping. All three localties are from the base of the Lower Deltaic Series.

HOLOTYPE: V. 52136 in the British Museum (Natural History) London.

Description of the material: There are two cotypes, one of the lower (or middle) part of a leaf, and one with long, narrow pinnules, which might be a very basal part of a leaf. And there are numerous small fragments.

COMPARISON: Although there are already numerous *Cladophlebis* species, the Yorkshire material, in my opinion, belongs to a new one.

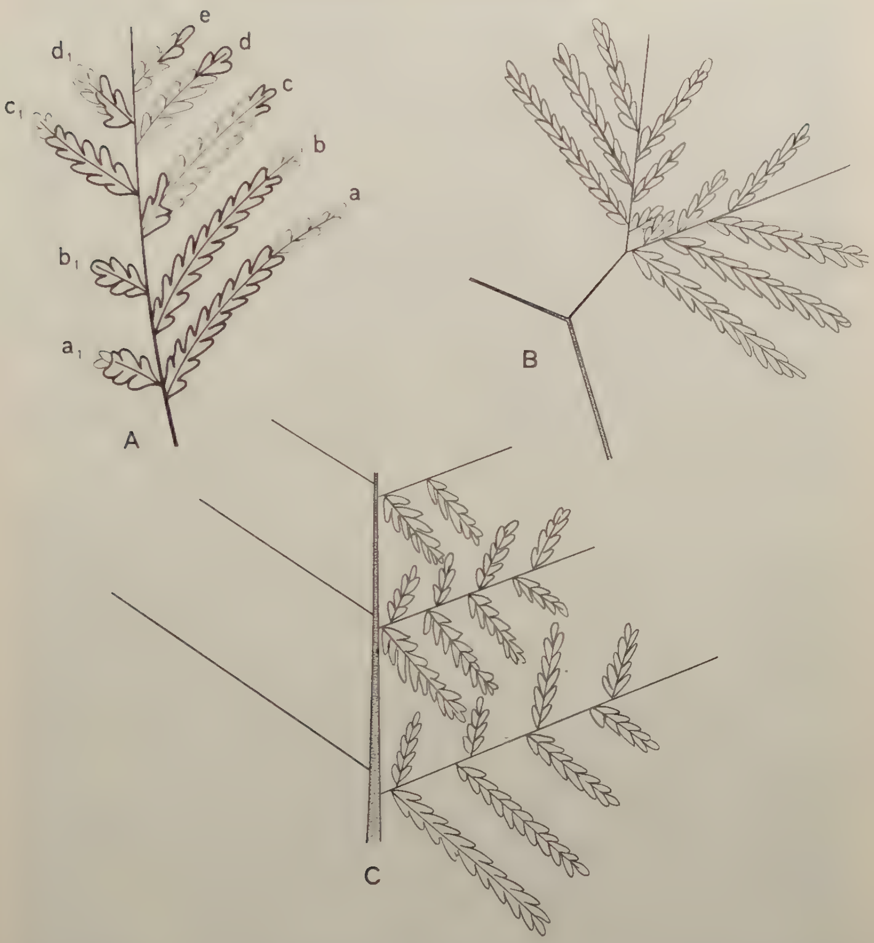


Fig. 1. *Cladophlebis harrisii* sp.n.
A. Drawing of the specimen from Plate I Fig. C, missing parts in weak lines.
B, C. Possible reconstructions of the frond.

There are some species that resemble this one in one or more aspects, but I do not think that anyone of them is conspecific with it.

Cladophlebis koraiensis Yabe (1905): Pinnules have the same variation in form but are unmistakeably smaller and they do not have the contraction at the base and the wing. Furthermore they are slightly dentate. The pinnae normally arise at a larger angle than in our specimens. The venation however is the same.

Cladophlebis zeylanica Sitholey (in: Sahni, 1942), Sitholey (1944): Again without the contracted base and the wing. In this case the pinnules are opposite. There are also many more lateral veins than in our specimens.

Cladophlebis tenue Oishi et Huzioka (1938), Oishi (1940): Pinnules more falcate and not so parallel-sided as in our specimens. Primary rachis much thinner, margin not exactly entire. Lateral veins always once forked, in our specimens seldom. The midrib always runs straight from close to the basal edge of the pinnule to the apex.

Cladophlebis spec. ∝ cf. *Thinfeldia arctica* (Heer) Seward (1907): Pinnules much larger and more apiculate, not so parallel-sided as in our material and without the contraction and wing. Midrib exactly in the middle of the pinnule. Lateral veins once forked and slightly sinous.

Cladophlebis denticalata Brgt. forma *atherstonei* (Tate) Seward (1903), Tate (1867): Pinnules arising at a much larger angle than in our specimens and also longer. Again without the contraction. Midrib exactly in the middle.

Cladophlebis parva Font. (1890), Berry (1911 a et b): Pinnae shorter and arising at a larger angle. Pinnules much shorter falcate and apiculate, separated to the base. The same variation in form of the pinnules as that in the new species.

Cladophlebis browniana (Dunker) Seward (1894), Dunker (1846), Seward (1903), Berry (1911), Yabe (1922): Rachis thinner. No contraction and wing. Pinnules often separated to the base. Lateral veins normally once forked, but sometimes twice or thrice and arising at a larger angle than in our material. Pinnules smaller and sometimes opposite. Lower pinnules lobed and falcate, which never occurs in our specimens.

Cladophlebis nebbensis (Brgt) Nathorst (1875), Nathorst (1878), Möller (1902), Yokoyama (1905), Seward (1907), Oishi (1940): Pinnules often dentate, broader than in the new species. Lateral veins sometimes twice forked, and arising at a larger angle. The bifurcation here is near the midrib and the midrib is in the middle of the pinnule.

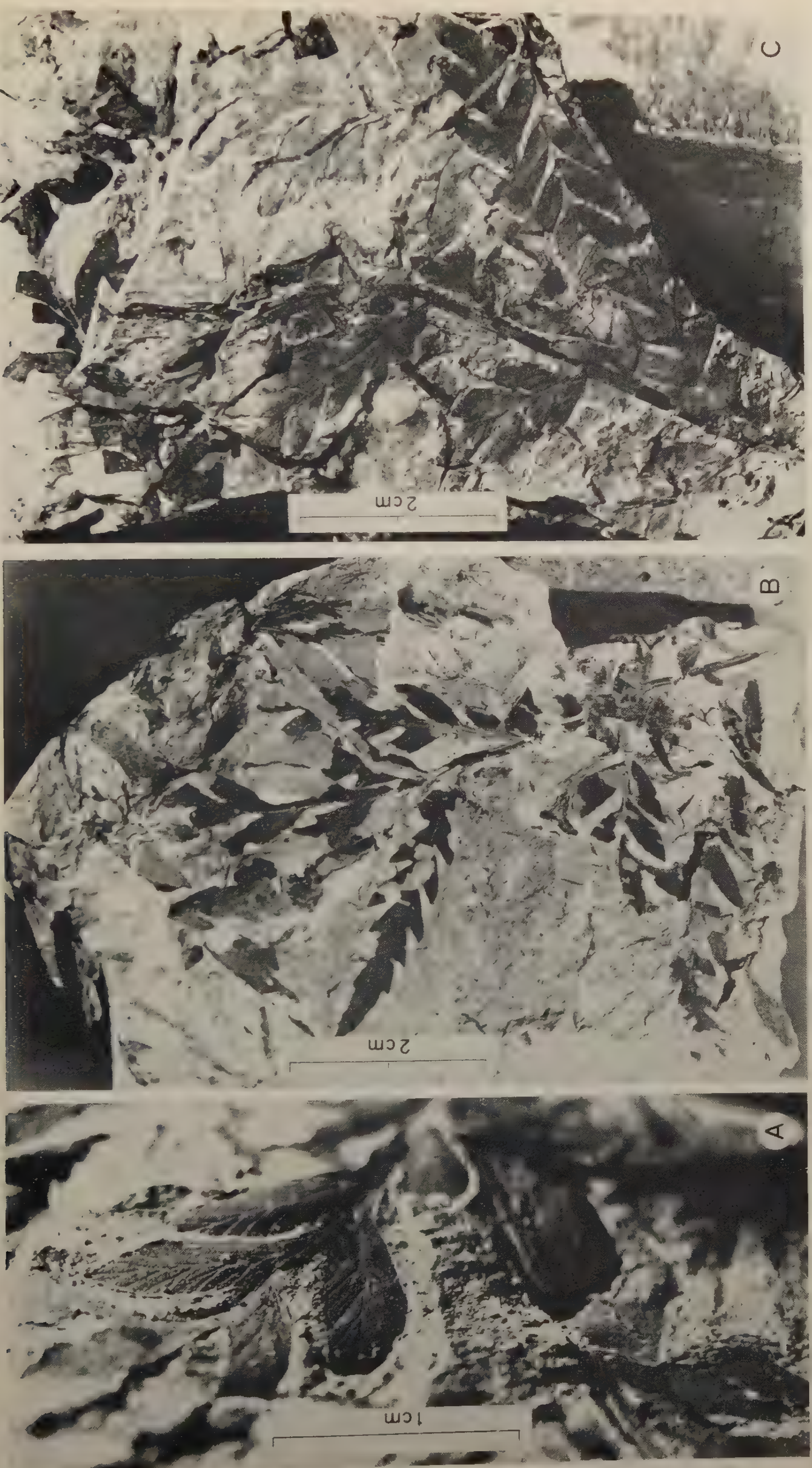
Cladophlebis pseudodenticulata Oishi (1932), Oishi (1940): Pinna-rachis very thin. Pinnules at right angles to the rachis, no contraction and wing. The venation is the same as in our specimens.

Discussion: In one of the specimens the pinnae on one side of the rachis become distally progressively smaller while those on the other side, originally smaller, increase in size until the pinnae on both sides of the rachis are of equal length. Subsequently they both become smaller. This specimen contains the lowest part of a leaf we have found until now (Plate I, Fig. C). This made us think about some possible reconstructions as shown in text-fig. 1. In both cases the fragments must belong to quite a large frond.

Note: In the present author's opinion the specimens listed by Harris (1961) under *Selenocarpus muensterianus* (Presl) Schenk also belong to this species.

Marattia anglica (Thomas) Harris Plate II, Fig. A

1913 *Marattiopsis anglica* Thomas p. 228, pl. 23 figs. 1–5, t. fig. 1
1961 *Marattia anglica* Harris 1 p. 72 text-fig. 23

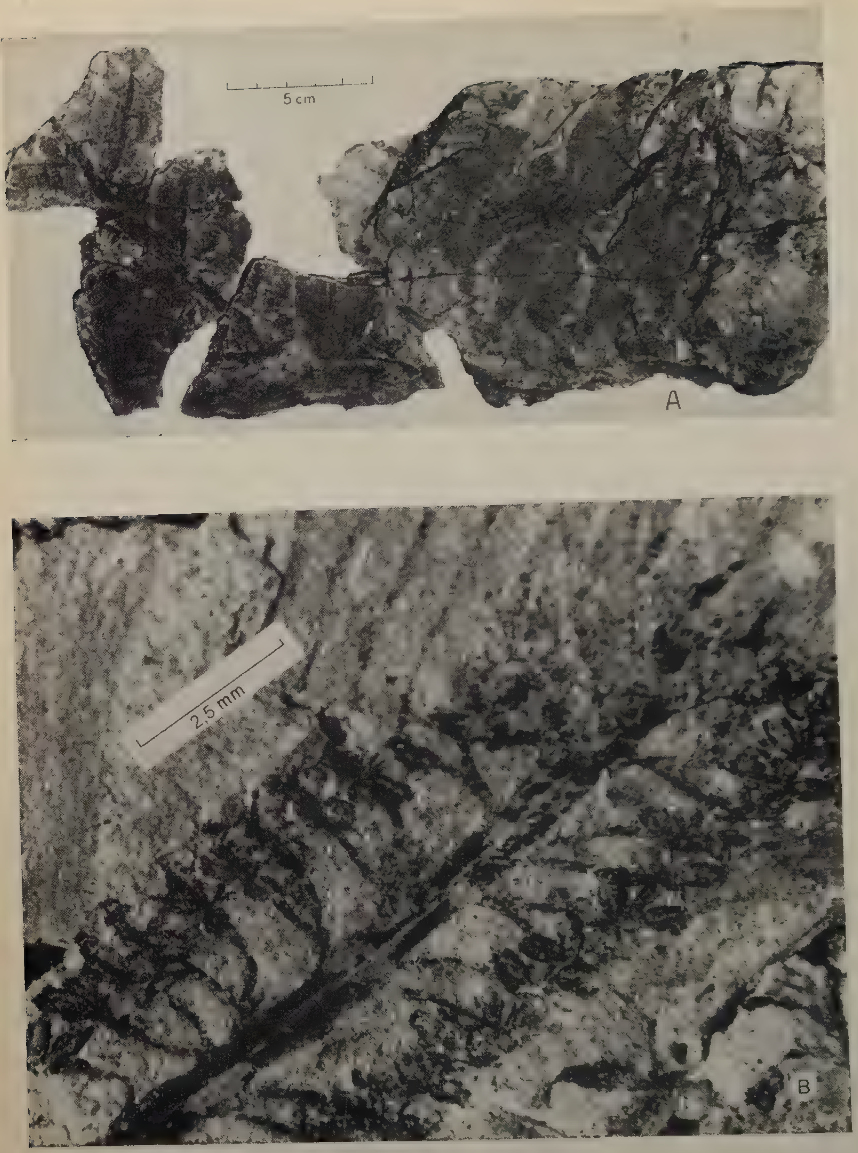


Cladophlebis harrisii sp.n.

A. pinnules of the middle part of the frond. V. 52136 B. holotype V. 52136

C. cotype van Cittert no. 1623 in Palaeobotany Division, Botanical Museum and Herbarium, Utrecht (*Photo F. de Vries*)

PLATE I



A. *Marattia anglica* (Thomas) Harris: part of frond with primary and secondary rachis (Ash, Harris and van Cittert no. 1615a in Palaeobotany Division, Botanical Museum and Herbarium Utrecht).
B. *Angiopteris neglecta* sp.n.: holotype no. 1371 in Palaeobotany Division, Botanical Museum and Herbarium, Utrecht. (*Photo F. de Vries*)

PLATE II

Supplementary diagnosis: Primary rachis at least 1½ cm thick, with irregular longitudinal ridges (striate), no hairs seen. Secondary rachis 5 mm thick, arising at an angle of 40° (no basal swelling observed, no hairs seen on the rachis). Ultimate divisions of lamina arising both on primary rachis between secondary rachises and on secondary rachises. Base of pinnae on the primary rachis contracted, midrib arising at an angle of 30° from the rachis, very soon bending outwards till 90° or more. Pinna-base on the secondary rachis contracted, midrib arising at an angle of 50° and going straight on.

Discussion: From some recent *Angiopteris* and *Marattia* species it is known that, sometimes, one or more pinnae divide into a secondary rachis with pinnae. And this could be the same in our specimen. I know of no other explanation for the fact that there are pinnae on the primary rachis too. It is a pity that the fossil is broken just above the secondary rachis, so that one can not see if there are pinnae above it or not.

The pinna-base and part of rachis found by H. H. Thomas (1913) would be, according to the data mentioned above, a secondary rachis and pinna. The present specimen differs from that one in that the pinna arises at a much larger angle: 75°, but this, I think, may be possible within one species.

Distribution: The specimen figured (Plate II, Fig. A) and described above was collected at Hasty Bank, Lower Deltaic by Ash, Harris and van Cittert, and is preserved in the Division of Palaeobotany of the Botanical Museum and Herbarium, Utrecht (no. 1615).

Angiopteris neglecta sp.n. Plate II, Fig. B.

Diagnosis: Fertile pinna 6 mm wide. Midrib 1 mm wide, longitudinally grooved. Lateral veins arising at an angle of about 60° and bending outwards to 90°, mostly forking once near the midrib; free ends not curving forwards; concentration at margin about 13 per cm. Venuli recurrentes apparently absent. Every branch bearing at its end a sorus, of about 6 sporangia. Sorus oval, 1½ mm long and so occupying half of the width of the lamina. Sporangia ovoid, up to 1 mm long.

Type specimen: no. 1371 in the Division of Palaeobotany of the Botanical Museum and Herbarium, Utrecht.

Occurrence: Hasty Bank-Lower Deltaic.

Discussion: There is only a single fragment of a fertile pinna.The specimen however looks so different from anything else found at Hasty Bank, that I feel entitled to describe it as a new species. It occurs in the same layer as *Marattia anglica* (Thomas) Harris 1961, Thomas 1913, but instead of having synangia this specimen has sori composed of separate sporangia which are loose enough to be displaced. And in *Marattia anglica* most of the veins appear simple, but in *Angiopteris* each one forks. The sporangia appear to be empty and there is so little material that I did not try to get spores out of it.

While fossils fairly close to *Marattia* are familiar we know very little indeed about the Mesozoic allies of *Angiopteris*. There is Schimper's genus *Angiopteridium*, with its type species *A. muensteri* (Goeppert) Schimper 1869. Schimper changed his mind about it, for he based his genus *Marattiopsis* on this species. Most of the other species of *Angiopteridium* fall into two groups: Several, like *A. angustifolium* (Schenk) Schimper 1869, *A. ensis* Oldham 1862, *A. spathulum* (McClelland) Schimper 1869, were previous to Schimper considered to belong to *Taeniopteris*. As there is no evidence of Marattiaceous sori, later authors have restored them to *Taeniopteris*. On the other hand the second group of species – like the type species *A. muensteri*, and *A. hoerense* Schimper 1869 –, which most authors consider closely related to *Marattia* with regard to the sori, are included in *Marattia* or its fossil equivalent *Marattiopsis*.

Whether *A. californicum* Fontaine (1896, 1900) from the Jurassic, which does appear to have Marattiaceous sori, has separate sporangia as in the present fern is yet to be made clear. FONTAINE gives no details. Until *Angiopteris*-like sori in Fontaine's species are established, *Angiopteris neglecta* is the only fossil *Angiopteris* known.

In my opinion this species must be classified with *Angiopteris* and not with *Angiopteridium* as it agrees in all known characters with *Angiopteris* whereas the status of *Angiopteridium* is not at all clear.

NOTE: Dr. K. U. Kramer suggested the relationship between this Jurassic fern specimen and the recent genus *Angiopteris*.

ACKNOWLEDGEMENTS

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POLLEN MORPHOLOGY OF SOME EUROPEAN ROSACEAE

TJ. REITSMA

(*Botanical Museum and Herbarium, Utrecht*)

(*received February 17th, 1966*)

Abstract

In this preliminary investigation attention was paid to pollen morphology of West-European species of the Rosaceae. Some new terms were used like fastigium, endocingulus etc. The terminology of Iversen and Troels-Smith has been followed in addition to improvements by Erdtman. A key is given to the types and subtypes for the use of pollen analytical investigators. *Sanguisorba officinalis* appeared to be always 3-colporate and not 6-colporate.

1. Introduction

It is well known that different types of pollen grains are found in the *Rosaceae*. Faegri and Iversen (1964) mention some in their key to the N.W. European pollen types, e.g. *Crataegus* type, *Potentilla* type, *Geum* type. From pollen analytical investigations there appear to be more present types than the three above.

The object was to form pollen morphological types, which are easily distinguishable from each other by constant differences. These types have been worked up into a key for the use of pollen analytical investigators.

Within the types it was sometimes possible to give a key to the included genera or species. In these keys use is made of less constant and distinctive differences such as the length, the shape etc.

2. Materials and methods

2.1. *Flowers*

Pollen grains were obtained from herbarium material at the Botanical Museum and Herbarium of Utrecht, and from freshly collected flowers. Only flowers which just bloomed or are about to bloom are useful.

2.2. *Treatment of the pollen grains*

Pollen grains from fresh flowers were treated with the acetolysis-method of Erdtman (1943). If only a little material was present and this is especially so in the case of herbarium material, the micro-method described by Punt (1962) has been used.

2.3. *Preservation*

For the preservation of the grains the paraffin-method with the improvements by Punt (1962) has been used, viz. the use of a granule of clay to support the cover-glass. This prevents large grains from being compressed.

2.4. *Microscopes*

The pollen grains have been studied with a Leitz Ortholux binocular (obj. pl. apo öl 100/1.32, oc. periplan 10 ×) and an Olympus phase-contrast microscope. This microscope was found very useful in detecting the configuration of the structural elements.

2.5. *Drawings*

The pollen grains have been drawn in such a manner that in one drawing as many characters as possible are to be seen at the same time. Each drawing therefore is midway between scheme and a photographical reproduction. The pollen grains have been drawn to scale, without a camera lucida or other drawing instruments.

The enlargment is 2000 × except *Mespilus* viz. 1000 ×.

2.6. *Photographs*

Microphotographs were made with a Leitz Orthomatcamera and Ortholux microscope apochr. obj. × 40, × 63 and an eyepiece × 10.

3. TERMINOLOGY

In principle the terminology of IVERSEN and TROELS-SMITH (1950) has been followed, although in addition improvements by Erdtman have been used (see also PUNT, 1962). At the same time some terms have been used, which need a new or altered description:

Aperture (FAEGRI and IVERSEN, 1950)
  A thinning or missing of a part of the sexine or nexine
COLUMELLAE INDEX-C.I.
  The ratio between the maximum height of the exine to the maximum height of the columellae
Costa pl. *costae* (FAEGRI and IVERSEN, 1950)
  Thickenings of the nexine
  Costae colpi: Thickened nexine below the edge of colpi
  COSTAE ENDOCINGULI: Thickened edges of the endocingulus
  COSTAE ENDOCOLPI: Thickened edges of the endocolpus
  COSTAE ENDOPORI: Thickened edges of the endoporus
  Costae pori: Thickened nexine below the edge of pori
Ectoaperture (VAN CAMPO, 1958)
  A thinning or a missing of a part of the sexine e.g. colpus, porus
Endoaperture (VAN CAMPO, 1958)
  A thinning or a missing of a part of the nexine
ENDOCINGULUS
  Endoaperture, forming a band round the equator, of which the diameter is perpendicular to the axis of the ectoaperture.
Endocolpus (ZAGWIJN, 1963)
  Endoaperture, of which one of the axes of the aperture is perpendicular to an axis of the ectoaperture. Length: breadth > 2

Endoporus (Zagwijn, 1963)
Endoaperture, of which one of the axes of the aperture is perpendicular to an axis of the ectoaperture. Length: breadth > 2

Membrana granulata (Erdtman, 1952)
Colpus or porus membrane (= nexine) with some scattered structural elements.

Membrana nudata (Erdtman, 1952)
Colpus or porus membrane (= nexine) without structural elements

Nexine (Erdtman, 1948)
The inner, non-sculptured part of the exine

Sexine (Erdtman, 1948)
The outer sculptured part of the exine

Fastigium pl. Fastigia (= Atrium Punt, 1962)
Cavity, inside colporate grains, caused by the separation of the nexine and the domed sexine in the area of the endoapertures. Punt (1962) named this an atrium. This term, however, has been used by Pflug in a publication by Thomson and Pflug (1953) for triporate Tertiary pollen grains. Consequently it is not advisable to use this term here.

The shapes of the pollen grains in polar and equatorial view are described according to the system of Kuyl, Muller and Waterbolk (1955).

The system of Erdtman (1952), which is based on the relation between the polar axis and the equatorial axis (P:E) in equatorial view, is also used.

The length of the longest axis has been indicated in the description. This measurement, which may be either the equatorial or the polar axis, is an exact indication of the size of the pollen grain.

Key to the types

1 a	Pollen grain with striae	2
b	Pollen grain without striae, that is psilate, echinate, scabrate, or only with phase contrast microscope striate	7
2 a	Pollen grain operculate	3
b	Pollen grain not operculate	4
3 a	Pollen grain without costae colpi	**Potentilla type**
b	Pollen grain with costae colpi	**Rosa gallica type**
4a	Striae indistinct, intrastriate	5
b	Striae distinct, extrastriate	6
5 a	Pollen grain with costae colpi	**Rubus idaeus type**
b	Pollen grain without costae colpi	**Crataegus type**
6 a	Pollen grain with tectum	**Geum type**
b	Pollen grain with tectum perforatum	**Mespilus type**
7 a	Pollen grain without structural elements on tectum	8
b	Pollen grains with structural elements on tectum	12
8 a	Pollen grain operculate	9
b	Pollen grain not operculate	10
9 a	C.I. > 4, pollen grain with costae colpi	**Rosa canina type**
b	C.I. < 3, pollen grain without costae colpi	**Sanguisorba type**
10 a	C.I. < 3, columellae in intercolpium higher than those at the poles	**Alchemilla type**
b	C.I. > 4, columellae in intercolpium as high as those at the poles	11

11 a Pollen grain with costae colpi . . . . **Rubus idaeus type**
b Pollen grain without costae colpi . . . . **Crataegus type**
12 a Structural elements small: scabrae; endocolpus . . . **Filipendula type**
b Structural elements large: echinae, gemmae, or verrucae; endoporus . . . . **Rubus chamaemorus type**

4. RESULTS

4.1. *General*

The pollen grains of the studied *Rosaceae* show a number of types, which can be distinguished clearly from each other. However, they all represent variations on the same theme.

They all are tricolporate. That both tricolpate and stephanocolporate pollen grains occur, can be looked upon as a normal variation.

The shape in equatorial view varies from prolate ($P:E = 1.33–2$) to suboblate ($P:E = 0.88–0.75$) and is mostly oval to rhomboidal. In some cases the shape is rectangular to compressed oval (*Alchemilla* type). The shape in polar view is mostly circular to semiangular, sometimes intersubangular (*Alchemilla* type) or subangular (*Mespilus* type). The colpi are usually narrow, sometimes broad (*Sanguisorba officinalis* subtype). In some types the colpi are accompanied by costae colpi (*Alchemilla* type, *Rosa canina* type, *Rosa gallica* type, *Rubus idaeus* type). Opercula can be present (*Potentilla* type, *Sanguisorba* type, *Rosa canina* type, *Rosa gallica* type). The polar area index (P.A.I.) ranges from 0.1 to 0.55. Costae endocolpi or endopori are sometimes present (*Rosa rubiginosa* subtype, *Geum* subtype).

The *Rosaceae* studied are all striate, both extra- and intrastriate. The last structure is mostly only visible with the phase-contrast microscope. The striae on the tectum are formed by some strong, more or less fused, capita. Columellae, however, do not occur in striae. Mostly all the grains have a tectum, except *Mespilus*, which has a tectum perforatum.

On the tectum structural elements of different shape may be found such as scabrae (*Filipendula* type), echinae, verrucae or gemmae (*Rubus chamaemorus* type). All these grains have a fastigium, which is also found in other tricolporate grains e.g. *Sedum*, *Solanum*, *Fabaceae* p.p., *Apiaceae* p.p.

4.2. *Description and discussion*

Crataegus type (FAEGRI AND IVERSEN, 1964) **Figs. 1, 2**

Diagnosis: tricolporate; fastigiate; psilate; intrastriate, mostly only visible with phase contrast; C.I. > 4; subprolate-suboblate; eq. view: oval-rhomboidal; pol. view: circular-semiangular; max. length: 23–42 μ.

Absent: operculum; costae colpi.

Species studied

Crataegus monogyna Jacq.	33912B, [U]; Gulperberg
Crataegus oxyacantha L.	071886B, [U]; Utrecht
Aronia melanocarpa (Michx.) Ell.	Wassenaar
Sorbus aria (L.) Crantz	115592B, [U]
Sorbus aucuparia L.	Utrecht

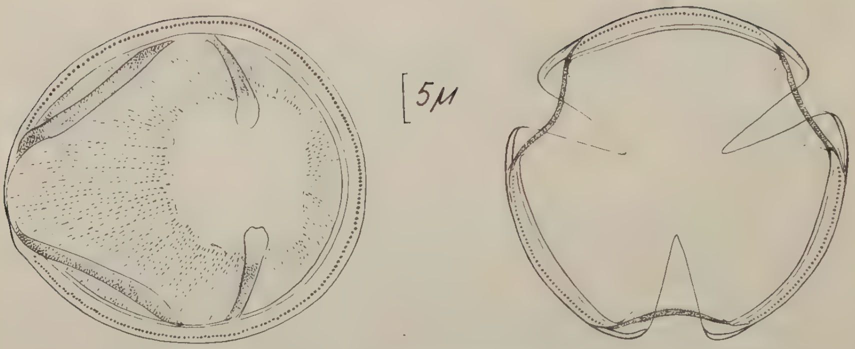


Fig. 1. *Crataegus monogyna Jacq.*

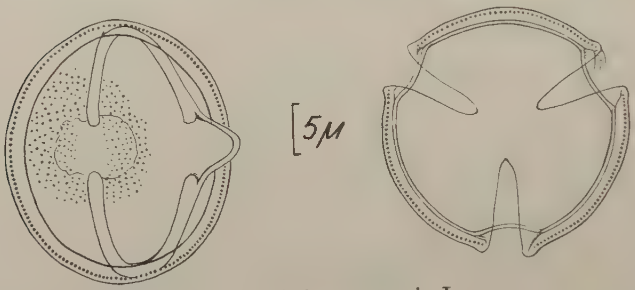


Fig. 2. *Sorbus aucuparia* L.

Mespilus type **Fig. 3**

Diagnosis: tricolporate (tricolpate); fastigiate; striate; tectum perforatum; C.I. > 4; oblate spheroidal-prolate spheroidal; eq. view: oval-rhomboidal; pol. view: circular-subangular.

Absent: operculum; costae colpi.

Species studied

Mespilus germanica L. 011015 [U]; Onderste Bos (Epen)

P.A.I.: 0.2–0.3: maximum length: 42–49 μ.

Rubus idaeus type **Figs. 4, 5**

Diagnosis: tricolporate; fastigiate; psilate; intrastriate, mostly only visible with phase contrast; costae colpi; C.I. > 4; prolate spheroidal-subprolate; eq. view: oval rhomboidal; pol. view: circular.

Absent: operculum.

Key to the subtypes

1 a Pollen grain with costae endocolpi . . . . . **Rosa rubiginosa subtype**
1 b Pollen grain without costae endocolpi . . . . . **Rubus idaeus subtype**

Rubus idaeus subtype **Plate IA**

Diagnosis: max. length: 24–40 μ; P.A.I.: 0.1–0.35;
Species studied

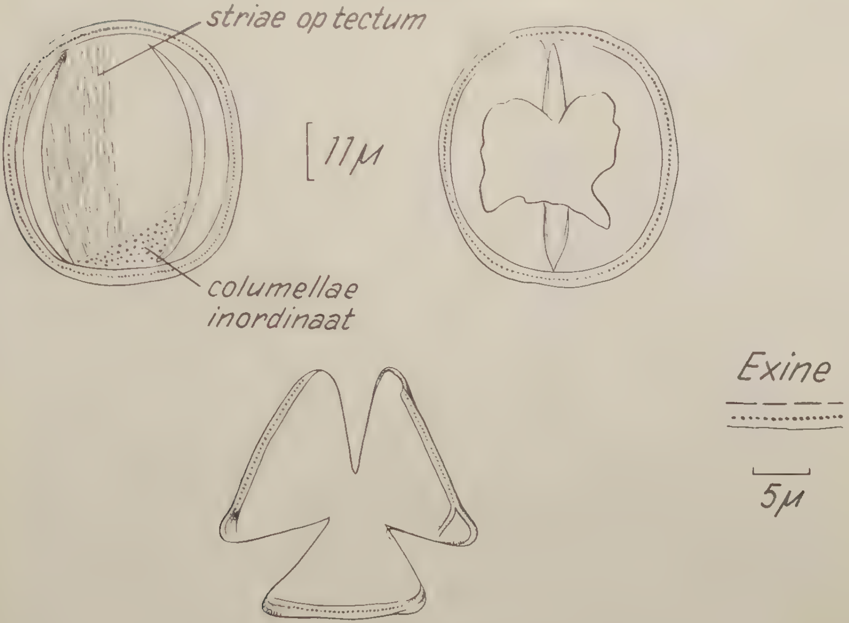


Fig. 3. *Mespilus germanica* L.

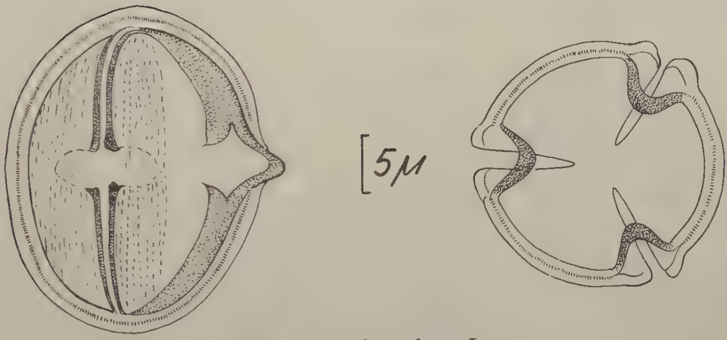


Fig. 4. *Rubus idaeus* L.

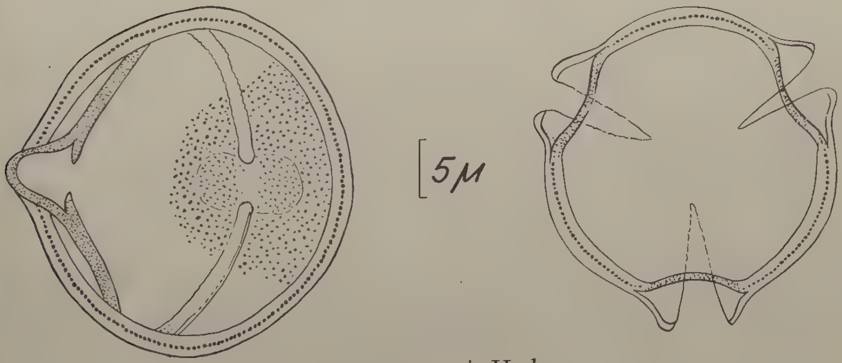


Fig. 5. *Rosa arvensis* Huds

Rubus idaeus L.	Bunde
Rubus saxatilis L.	J. Th de Smidt, Lapland N. 21
Rubus adornatus P. J. Mueller ex Wirtg.	093013B [U]
Rosa arvensis Huds.	Onderste Bos (Epen)
Rosa rugosa Thunb.	Utrecht

Rosa rubiginosa subtype

Plate IB; Fig. 6

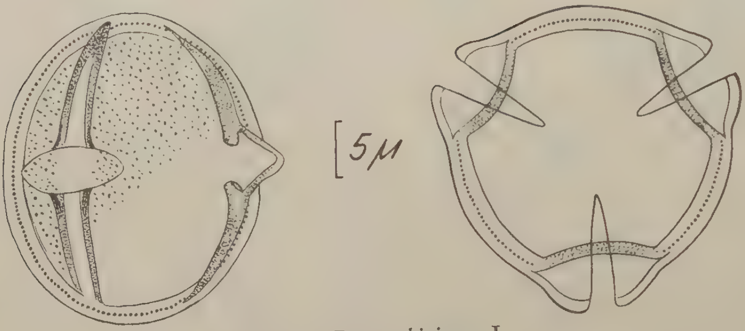


Fig. 6. *Rosa rubiginosa* L.

Diagnosis: max. length 28–32 μ; P.A.I.: 0.25–0.35

Species studied

Rosa rubiginosa L. Utrecht

Rubus chamaemorus type

Plate IE; Fig. 7

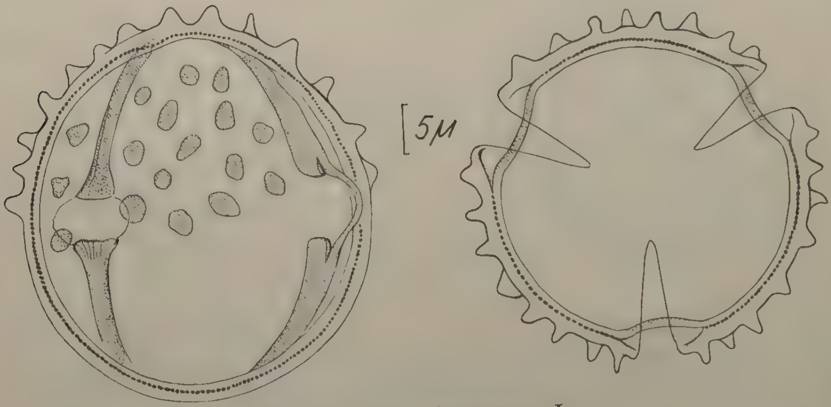


Fig. 7. *Rubus chamaemorus* L.

Diagnosis: tricolporate; fastigiate; echinate, verrucate, or gemmate; intrastriate, only visible with phase contrast; costae colpi; C.I. > 4; spheroidal-prolate spheroidal; eq. view: oval; pol. view: circular.

Absent: operculum.

Species studied

Rubus chamaemorus L. Herb. Lindeman et van Royen 140

Diagnosis: $m : e = 5\mu$; max. length: 35–41μ; P.A.I.: 0.25–0.32; structural elements: max. length 1.7μ, diameter 3.3μ.

Rosa canina type

Plate IC; Fig. 8

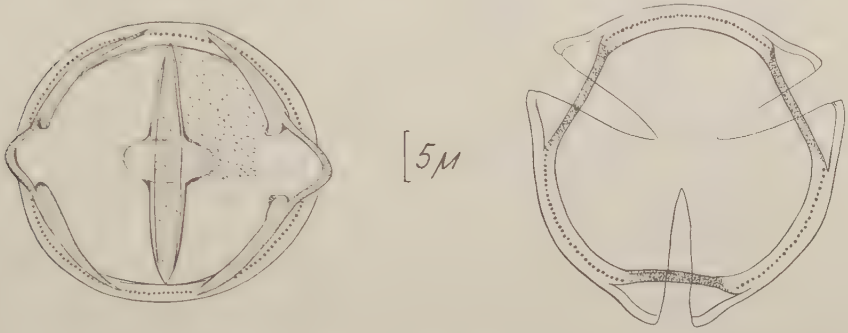


Fig. 8. *Rosa canina* L.

Diagnosis: tricolporate; fastigiate; psilate; intrastriate mostly only visible with phase contrast; costae colpi; costae endocolpi; operculate; C.I. $>$ 4; suboblate-oblate spheroidal; eq. view: oval-rhomboidal; pol. view: circular; max. length: 25–32μ; P.A.I.: 0.17–0.30.

Species studied

Rosa canina L.	Bunde

Rosa gallica type

Plate ID; Fig. 9

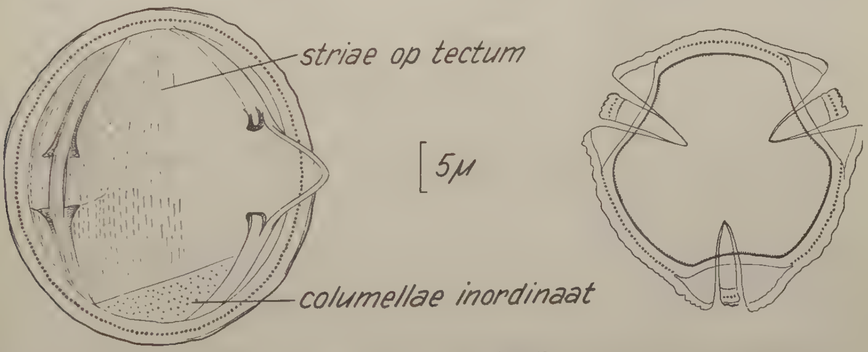


Fig. 9. *Rosa gallica* L.

Diagnosis: tricolporate; fastigiate; striate; costae colpi; operculate; C.I. $>$ 4; oblate spheroidal-prolate spheroidal; eq. view: oval-rhomboidal; pol. view: circular; max. length: 27–34; P.A.I.: 0.25–0.35.

Species studied

Rosa gallica L.	Yougoslavia

Potentilla type (Faegri and Iversen, 1964)

Diagnosis: tricolporate (stephanocolporate); fastigiate; striate; operculate; C.I. $>$ 4; prolate spheroidal-prolate; eq. view: oval-

rhomboidal; pol. view: circular-semiangular-interhexagonal-subangular; P.A.I.: 0.1–0.4.
Absent: costae colpi.

KEY TO THE SUBTYPES

1 a Tectum at the pole and in the intercolpium of uniform breadth . . . 2
b Tectum at the pole twice as broad as in the intercolpium . . . . **Potentilla sterilis subtype**
2 a Striae anastomosing . . . . **Fragaria vesca subtype**
b Striae not anastomosing 3
3 a Operculum protruding from the fastigium . . . . **Comarum palustre subtypes**
b Operculum not protruding from the fastigium . . . . **Potentilla anserina subtype**

Potentilla sterilis subtype

Plate I F; Fig. 10

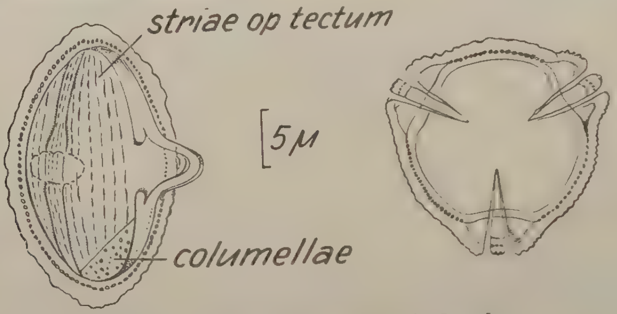


Fig. 10. *Potentilla sterilis* (L.) Garcke

Diagnosis: $m : e = 0.5–0.7$; max. length: 22–32μ; eq. view: oval-rhomboidal; pol. view: circular-semiangular.

Species studied

Potentilla sterilis (L.) Garcke	Sötenich (Germany)
Potentilla recta L.	42002A [U]
Potentilla intermedia L.	Sötenich (Germany)

Comarum palustre subtype

Plate I G; Fig. 11

Diagnosis: $m : e = \pm 0.5$ max. length 21–27μ; eq. view: oval; pol. view: circular-interhexagonal.

Species studied

Comarum palustre L.	Loosdrecht; Terschelling; Maarsseveen

Discussion

Following SCOPOLI (1772), BAILLON (1869), BENTHAM and HOOKER (1865), FOCKE (1888) and WOLF (1908) transmit the genus *Comarum* to the genus *Potentilla*: *Potentilla palustris* (L) Scop.

This is perfectly justified by the pollen morphological results.

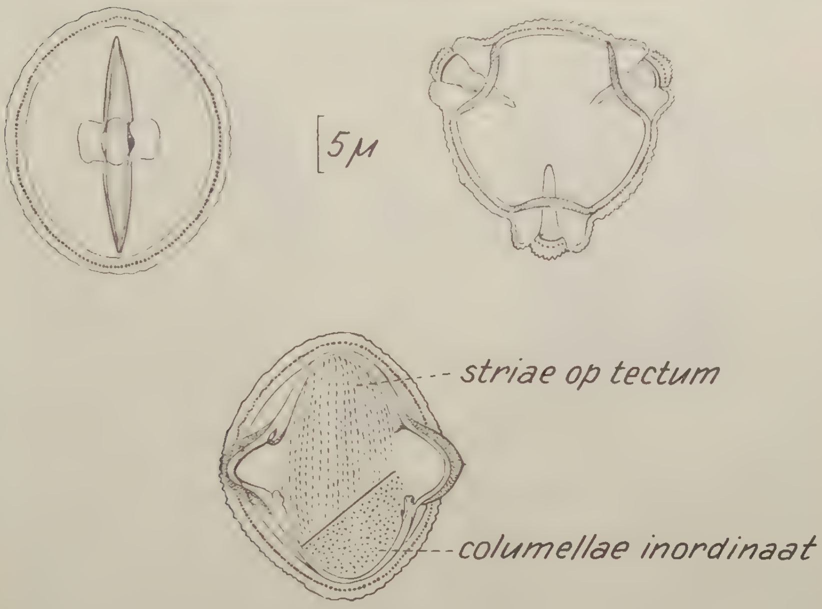


Fig. 11. *Comarum palustre* L.

Fragaria vesca subtype **Fig. 12**

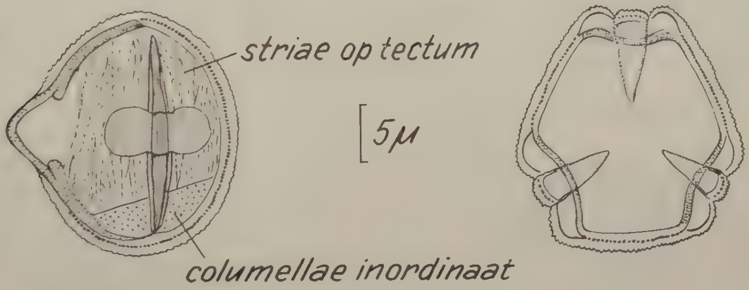


Fig. 12. *Fragaria vesca* L.

KEY TO THE SPECIES

1 a Longest axis 18–25 μ; endocolpus; $m : e = 0.2$–0.4 2
  b Longest axis 25–31 μ; endoporus; $m : e = 0.5$–0.75. 3
2 a Pol. view: interhexagonal . . . . **Fragaria vesca**
  b Pol. view: circular . . . . **Potentilla reptans**
3 a Pol. view: subangular . . . . **Fragaria moschata**
  b Pol. view: circular . . . . **Potentilla tabernaemontani**

Species studied

Fragaria moschata Duch.	105106B [U]
Fragaria vesca L.	Utrecht
Potentilla tabernaemontani Aschrs.	Bemelerberg
Potentilla reptans L.	Rhenen; Maarn

Potentilla anserina subtype

Plate IIA; Fig. 13

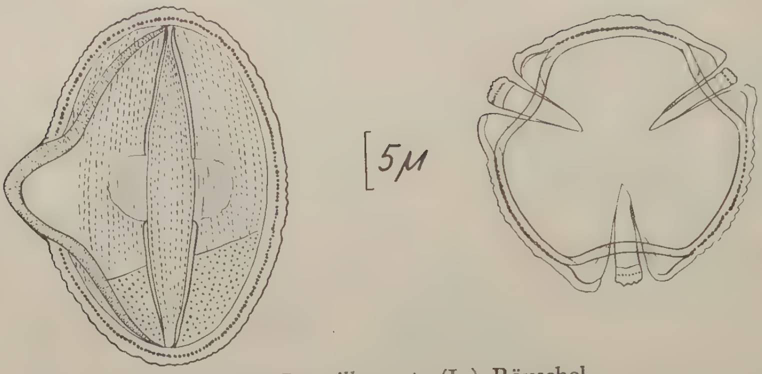


Fig. 13. *Potentilla erecta* (L.) Räuschel

Diagnosis: $m : e = \pm 0.5$; longest axis 22–38μ; eq. view: oval; pol. view: circular.

Species studied

Potentilla anserina L.	Westbroek; Utrecht
Potentilla argentea L.	Hilversum; Dortenbachtal (Germany)
Potentilla anglica Laich	149472B, [U]
Potentilla erecta (L.) Räuschel	Ginkelse heide; Maarn
Potentilla norvegica L.	Hilversum; 09644B [U]

Geum type (Faegri and Iversen, 1964)

Diagnosis: tricolporate; fastigiate; striate; C.I. > 4; suboblate-prolate; eq. view: oval-rhomboidal; pol. view: circular-semi-angular.

Absent: operculum; costae colpi.

Key to the subtypes

Costae endocolpi present	**Geum subtype**
Costae endocolpi not present	**Dryas subtype**

Geum subtype

Plate IIB; Figs. 14, 15

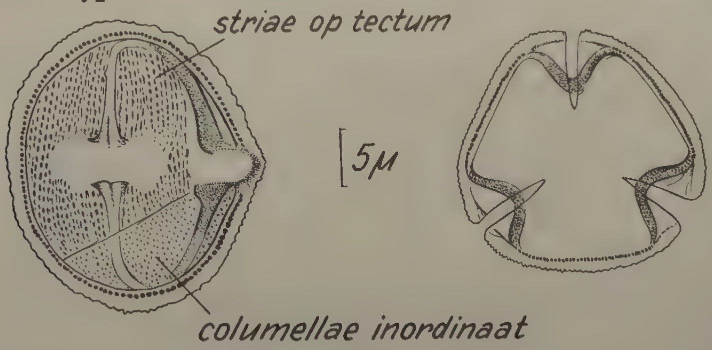


Fig. 14. *Geum urbanum* L.

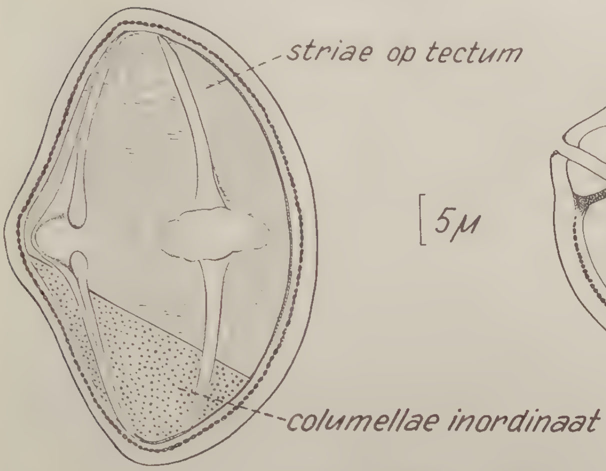


Fig. 15. *Agrimonia eupatoria* L.

Diagnosis: prolate spheroidal-prolate; eq. view: oval; pol. view: circular-semiangular; P.A.I.: 0.25–0.45.

KEY TO THE GENERA AND SPECIES

1 a longest axis 22–33 μ . . . .
b longest axis 35–60 μ . . . .
2 a longest axis 22–28 μ;*m*: 3–3.5 μ . . . . **Geum urbanum**
b longest axis 28–33 μ *m*: 2.2–2.8 μ . . . . **Geum rivale**
3 a longest axis 35–50 μ; thickness exine 2.8 μ . . . **Agrimonia eupatoria**
b longest axis 50–60 μ; thickness exine 3.5 μ . . . . **Agrimonia odorata**

Species studied

Geum urbanum L.	Utrecht
Geum rivale L.	Apeldoorn
Agrimonia eupatoria L.	Terziet
Agrimonia odorata L.	Th. H. ten Berge 526

Dryas subtype

Plate IIC; Figs. 16, 17

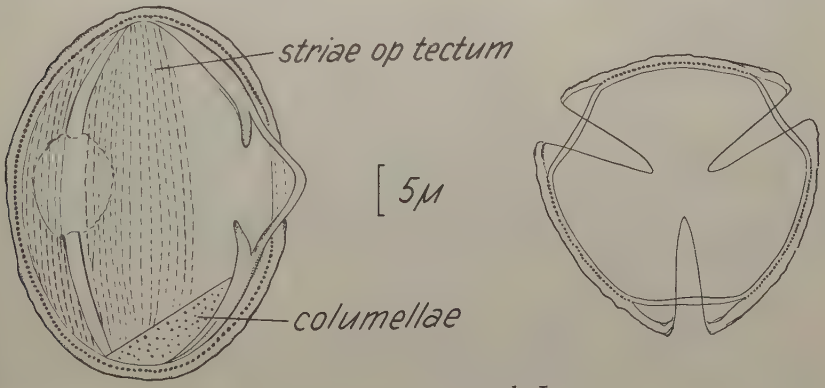


Fig. 16. *Dryas octopetala* L.

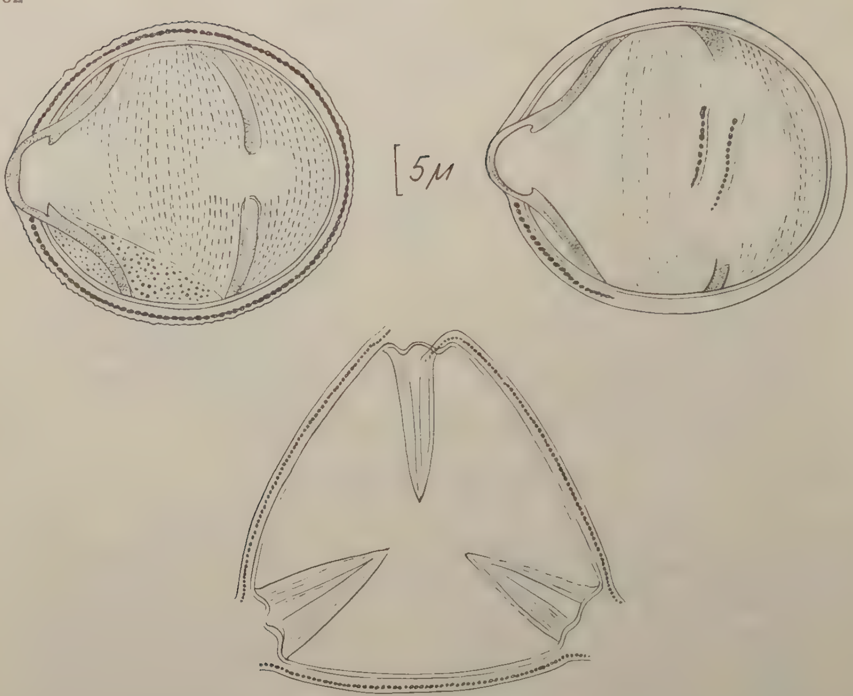


Fig. 17. *Prunus avium* L.

Diagnosis; suboblate-prolate spheroidal; eq. view: oval-rhomboidal; pol. view: circular; longest axis; 24–46μ; P.A.I.: 0.13–0.35.

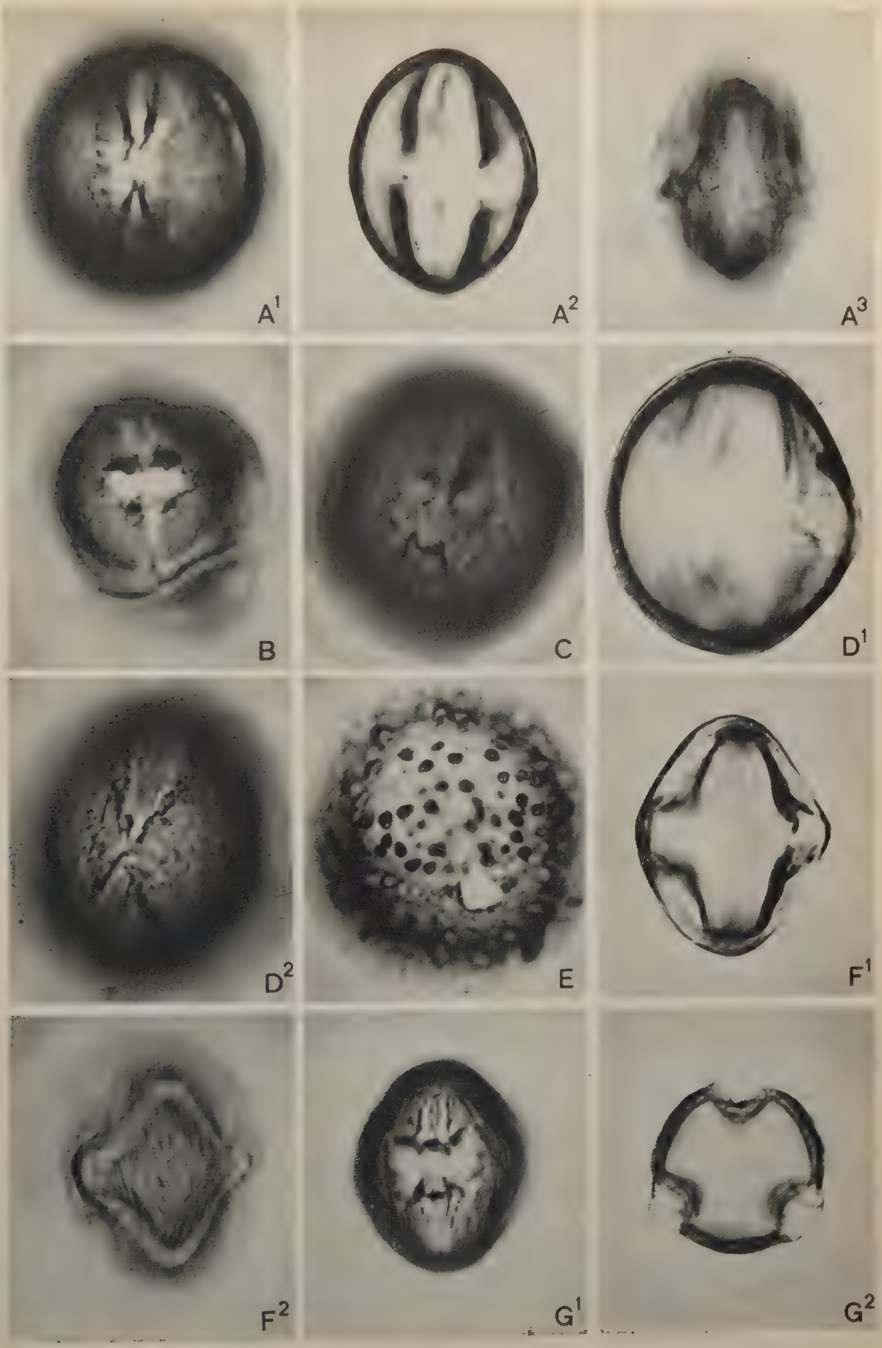
Species studied

Dryas octopetala L.	Leg. Stud. Biol. in itinere Helv. 109, 1913
Physocarpus opulifolius (L.) Maxim.	Culture
Prunus avium L.	Beek, Montferland
Prunus cerasus L. var. *austera* L.	Utrecht
Prunus spinosa L.	Utrecht
Prunus persica (L.) Batsch.	cult.
Prunus padus L.	Utrecht
Prunus serotina Ehrl.	Utrecht

Discussion

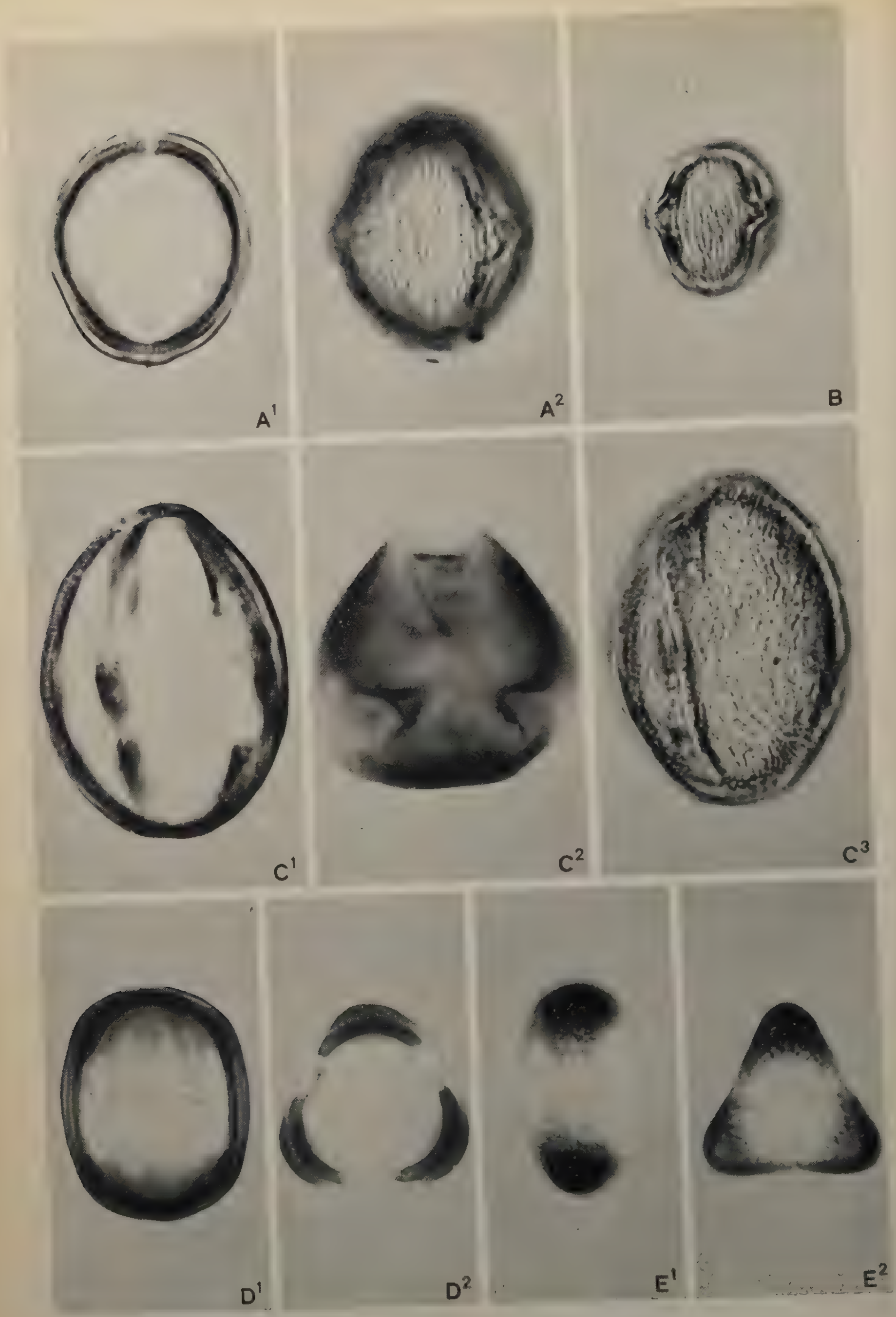
ERDTMAN, BERGLUND, and PRAGLOWSKI (1961), FAEGRI and IVERSEN (1964) and ERDTMAN (1943) give a description of *Dryas octopetala*. They all state that the longest axis is less than 25μ. The grains studied here, however, have a length of 30–36μ. It is known though, that the size of pollen grains can be depend on polyploidy (ERDTMAN 1963).

BÖCHER and LARSEN (1955) found in the Alps near Col du Pillon tetraploid forms of *Dryas octopetala*: $2n = 36$, beside diploid plants: $2n = 18$. Different authors like R. Czapik, in a publication of SKALINSKA *et al.* (1955) and LÖVE and LÖVE (1956) have found in the North only diploid plants: $2n = 18$.



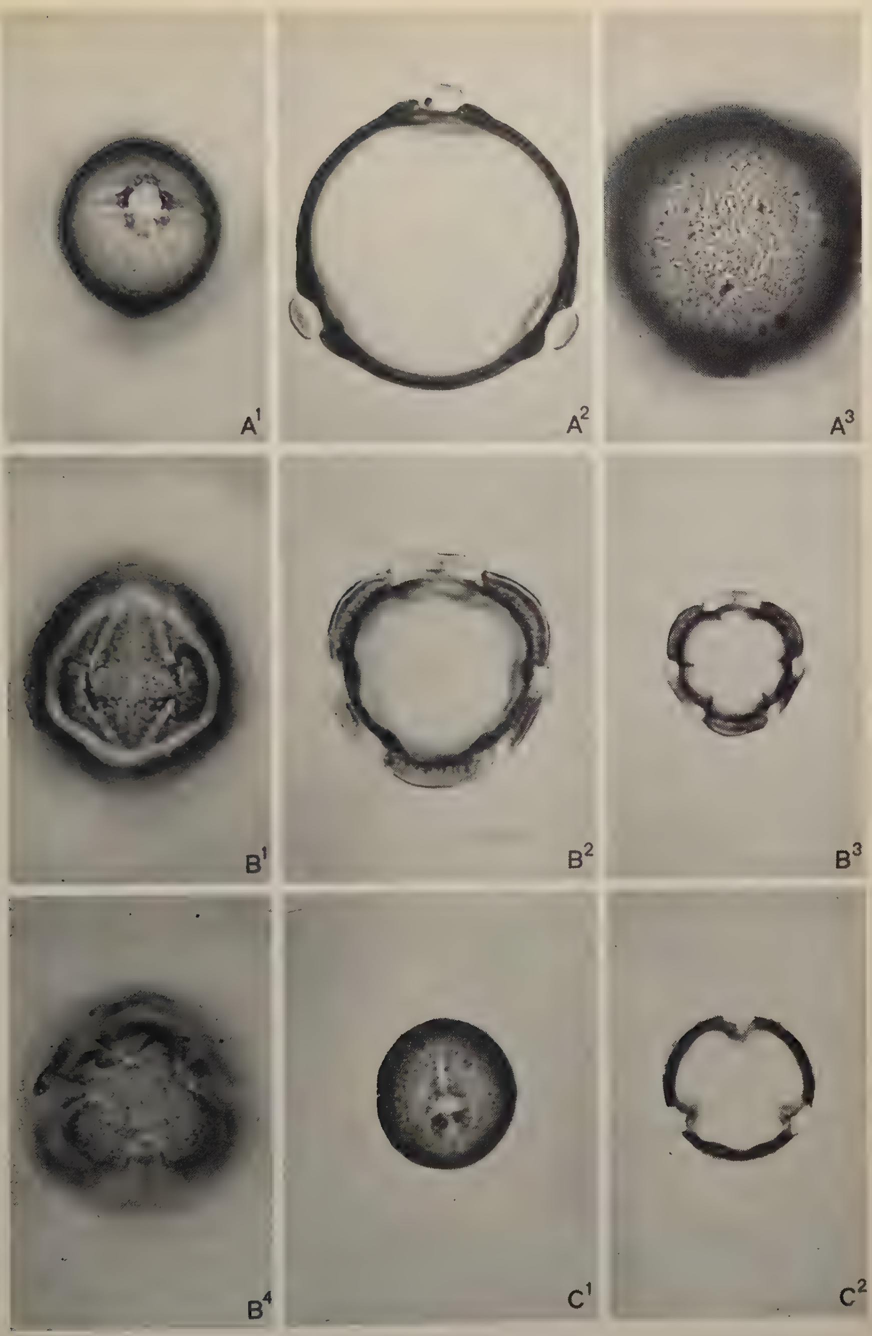
A^1 Rosa arvensis
$A^{2,3}$ Rubus idaeus
B Rosa rubiginosa
C Rosa canina
$D^{1,2}$ Rosa gallica
E Rubus chamaemorus
$F^{1,2}$ Potentilla sterilis
$G^{1,2}$ Comarum palustre

PLATE I



A^{1,2} Potentilla anserina
B Geum urbanum
C^1 Prunus cerasus
C^{2,3} Dryas octopetala
D^{1,2} Alchemilla glabra
E^{1,2} Aphanes arvensis

PLATE II



$A^{1,2,3}$ Sanguisorba minor
$B^{1,2,3,4}$ Sanguisorba officinalis
$C^{1,2}$ Filipendula ulmaria
PLATE III

Probably this is the reason that the axis is shorter in those grains previously examined.

A pollen morphological and cytological study is necessary to come to any conclusion.

Alchemilla type **Fig. 18**

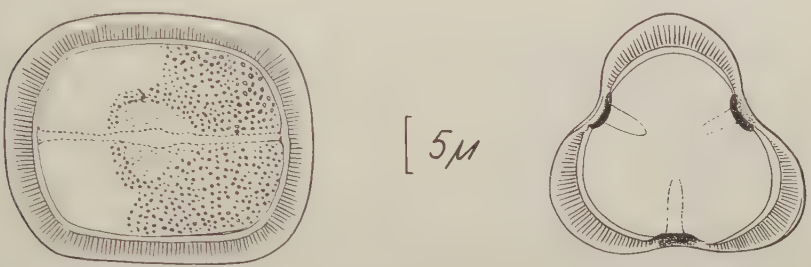


Fig. 18. *Alchemilla glabra* Neygens

Diagnosis: Tricolporate, sometimes tricolpate; fastigiate; Intrastriate, only visible with phase contrast; C.I. < 3; endoporus ± circular; columellae in intercolpium higher than those at the poles; subprolate-prolate; eq. view: rectangular-compressed oval; pol. view: intersubangular.

Absent: operculum

KEY TO THE SUBTYPES

Pollen grain with costae colpi; colpus membrane nudate . . . . **Alchemilla subtype**

Pollen grain without costae colpi; colpus membrane granulate . . . . **Aphanes subtype**

Alchemilla subtype **Plate IID**

Species studied

Alchemilla glabra Neygenf.	Reeuwijkse plassen

Aphanes subtype **Plate IIE**

Species studied

Aphanes arvensis L.	Gulperberg; Elslo

Diagnosis: Longest axis: 24–28μ; P.A.I.: 0.31–0.36.

Sanguisorba type

Diagnosis: tricolporate; fastigiate; psilate; intrastriate; mostly only visible with phasecontrast; operculate; C.I. < 3; oblate spheroidal-prolate spheroidal; eq. view oval-rhomboidal; pol. view circular

Absent: costae colpi

KEY TO THE SUBTYPES

1 a Maximum width of the colpus < maximum width of the intercolpium at equatorial view; pollen grain oblate spheroidal . . . . **Sanguisorba minor subtype**

b Maximum width of the colpus > maximum width of the intercolpium at equatorial view; pollen grain prolate spheroidal . . . . **Sanguisorba officinalis subtype**

Sanguisorba minor subtype — Plate IIIA; Fig. 14

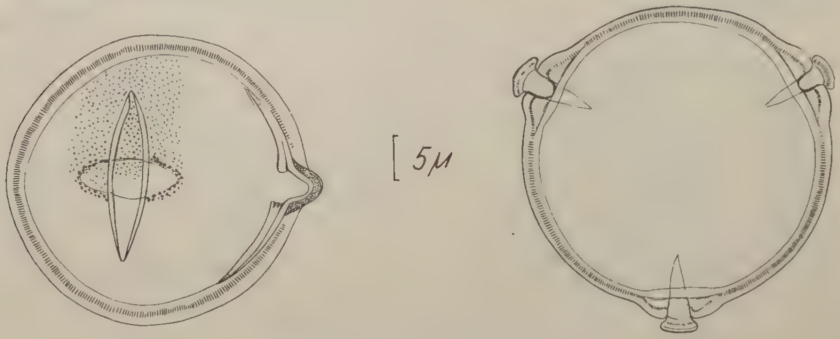


Fig. 19. *Sanguisorba minor* Scop.

Species studied

Sanguisorba minor Scop.	Pietersberg; Eyserbossen

Diagnosis: Longest axis: 32–39μ; P.A.I.: 0.41–0.55; end of the colpus distinct; acute.

Sanguisorba officinalis subtype — Plate IIIB; Fig. 20

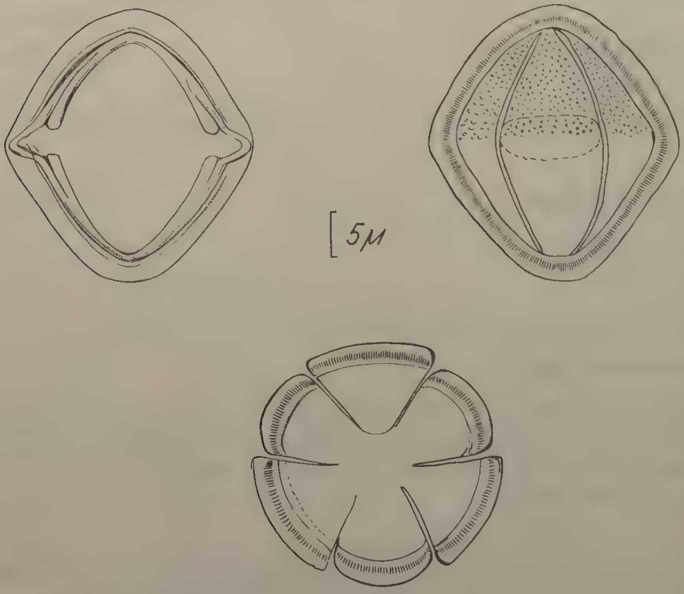


Fig. 20. *Sanguisorba officinalis* L.

Species studied

Sanguisorba officinalis L. Hardenberg, along the Vecht

Diagnosis: Longest axis: 28–32μ P.A.I.: 0.15–0.25.

Discussion

Pollen grains of *Sanguisorba officinalis* have been described mostly as 6-colporate (Faegri and Iversen (1964), Erdtman, Berglund and Praglowski (1961) and others). Erdtman and Nordborg (1961) and Erdtman (1963) indicate that tetraploid plants $2n = 56$ only produce 6-*colporate* forms and diploid plants $2n = 28$ both 6-*colporate* as 3-*colporate* forms.

In aperture pollen grains there are two different positions of the ectoaperture possible viz. situated opposite one other or not so. When the ectoapertures are opposite then the pollen grain has an even number of ectoapertures. When the ectoapertures are not opposite then the pollen grain has an odd number of ectoapertures.

This can be seen best in equatorial view when one of the ectoapertures is turned to the investigator as completely as possible.

The above mentioned condition does not apply to periporate, pericolpate and pericolporate pollen grains.

Studying pollen grains of *Sanguisorba* in such a manner, it is evident that the ectoapertures are not situated opposite one another. So the pollen grain must be tricolporate.

Also the situation of the 6 "colpi" in the pollen grain is strange viz. colpi at varying distances from each other. There are broad and narrow "intercolpia". When the two colpi with the broadest "intercolpium" are regarded as the colpus, there results a situation in which the ectoapertures are situated on uniform distance from each other, as is the case in all the remaining Rosaceous pollen grains studied. The end of the colpus is sometimes distinct. Than it is easy to see that the pollen grain possess 3 broad ectoapertures and 3 small intercolpia. It is clear now that, what was originally described as the colpus, is the nexine membrane between the edge of the colpus and the large operculum.

Filipendula type **Plate IIIC; Fig. 21**

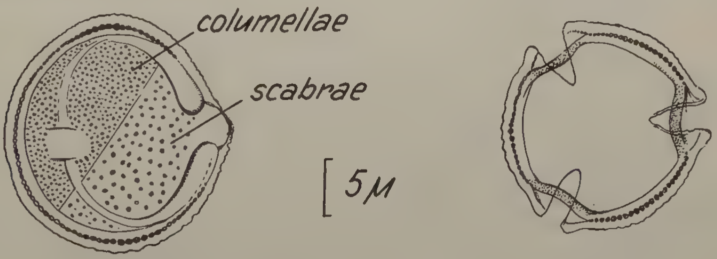


Fig. 21. *Filipendula ulmaria* (L.) Maxim.

Diagnosis: tricolporate; fastigiate; scabrate; intrastriate, only visible with phase contrast; C.I. $\gg$ 4; prolate spheroidal-subprolate; eq. view: oval-rhomboidal; pol. view: circular.

Absent: operculum; costae colpi.

Species studied

Filipendula ulmaria (L.) Maxim. Terziet

Diagnosis: max. length: 17–21μ; P.A.I.: 0.3–0.55.

Filipendula vulgaris Moench cult. Cantonspark

Diagnosis: max. length: 15–21μ; P.A.I.: 0.25–0.45.

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Acta Botanica Neerlandica **15** (1966) 308–315

EINIGE BEMERKUNGEN ÜBER DIE POLLENFÜHRUNG DER BRAUNKOHLENGRUBE "MARIA THERESIA", HERZOGENRATH

J. E. MEULENKAMP
(*Geologisches Institut, Utrecht*)

(*eingegangen am 14. März 1966*)

ABSTRACT

The pollenflora of the browncoal mined in the quarry "Maria Theresia", Herzogenrath, Western Germany has been investigated. Samples were taken along a section of 12.50 meters at intervals of 50 centimeters.

Identifications were made on the basis of form-genera and form-species; this working method gives a broad information on pollen types, but does not relate the fossil pollen types primarily to recent plant taxa.

Pollen types which are considered to belong to *Betulaceae/Myricaceae* make up the biggest part of the pollen assemblages.

The construction of a "Composite diagram" for *Betulaceae/Myricaceae* proved to be useful and might give a better idea on paleoecologic conditions.

The stratigraphic position of the browncoal examined is thought to be Lower "Hauptflöz", possibly Morken or Frimmersdorf Horizont.

EINLEITUNG

Es wurde eine pollenanalytische Untersuchung der Braunkohle der Grube "Maria Theresia", Herzogenrath, durchgeführt. Während der Probenentnahme standen 12.50 Meter an; es wurden 24 Proben bearbeitet, meistens in Abständen von 50 cm. Die Kohle erweist sich durch und durch als sehr holzreich; es konnten jedoch drei mehr oder weniger getrennte Stubbenhorizonte festgestellt werden (siehe das Diagramm). Auf 4.50 und 8 M finden sich 0.75, bzw. 0.50 M mächtige, sandige Einschaltungen.

Die Bearbeitung der Proben erfolgte unter der Leitung von Herrn Prof. Dr. F. P. Jonker im Institut für Systematische Botanik der Reichsuniversität Utrecht, Abteilung Paläobotanik und Pollenmorphologie.

Den Herren Dr. G. von der Brelie und seinen Mitarbeitern vom Geologischen Landesamt Nordrhein-Westfalen in Krefeld; Dr. W. Punt, Drs. J. van der Burgh und Dr. K. U. Kramer vom botanischen Institut Utrecht für Besprechen und kritisches Durchlesen des Manuskriptes ist Verfasser zu grossem Dank verpflichtet.

METHODIK

Die Aufbearbeitung der Proben fand folgendermassen statt:

1) 1–2 Gramm Braunkohle wurde zermahlen und etwa 10 Minuten mit 10 %-iger H_2O_2-Lösung erwärmt, dann mit Wasser gespült, zentrifugiert und dekantiert.
2) Wärmen mit 10 % KOH Lösung; zentrifugieren und dekantieren.
3) Spülen mit Wasser; zentrifugieren und dekantieren.
4) Glycerol-Lösung hinzufügen.

Die Proben erwiesen sich als pollenreich; es wurden im allgemeinen 200 Pollenkörner gezählt; mit Ausnahme von den meist stark korrodierten, sporadisch auftretenden Formen der Arten *Corrugatisporites* und *Laevigatosporites* wurden alle Formen in die Gesamtzahl von 200 mit einbezogen.

Für die Bestimmung wurde hauptsächlich THOMSON und PFLUG (1953) benützt. Da man bisher für viele tertiäre Pollenformen noch keinen eindeutigen Zusammenhang zu rezentem Pollen hat feststellen können, erscheint uns diese Arbeitsmethodik mit Formgattungen und Formarten als richtig.

POLLENFÜHRUNG (Pollendiagramm, Abb. 1)

Insgesamt wurden 65 Formarten und Unterarten unterschieden; die wichtigsten wurden in 11 Familien zusammengefasst, welche in das Diagramm eingetragen worden sind.

Betulaceae / Myricaceae

In allen Proben massenhaft vertreten. Am häufigsten fanden sich:

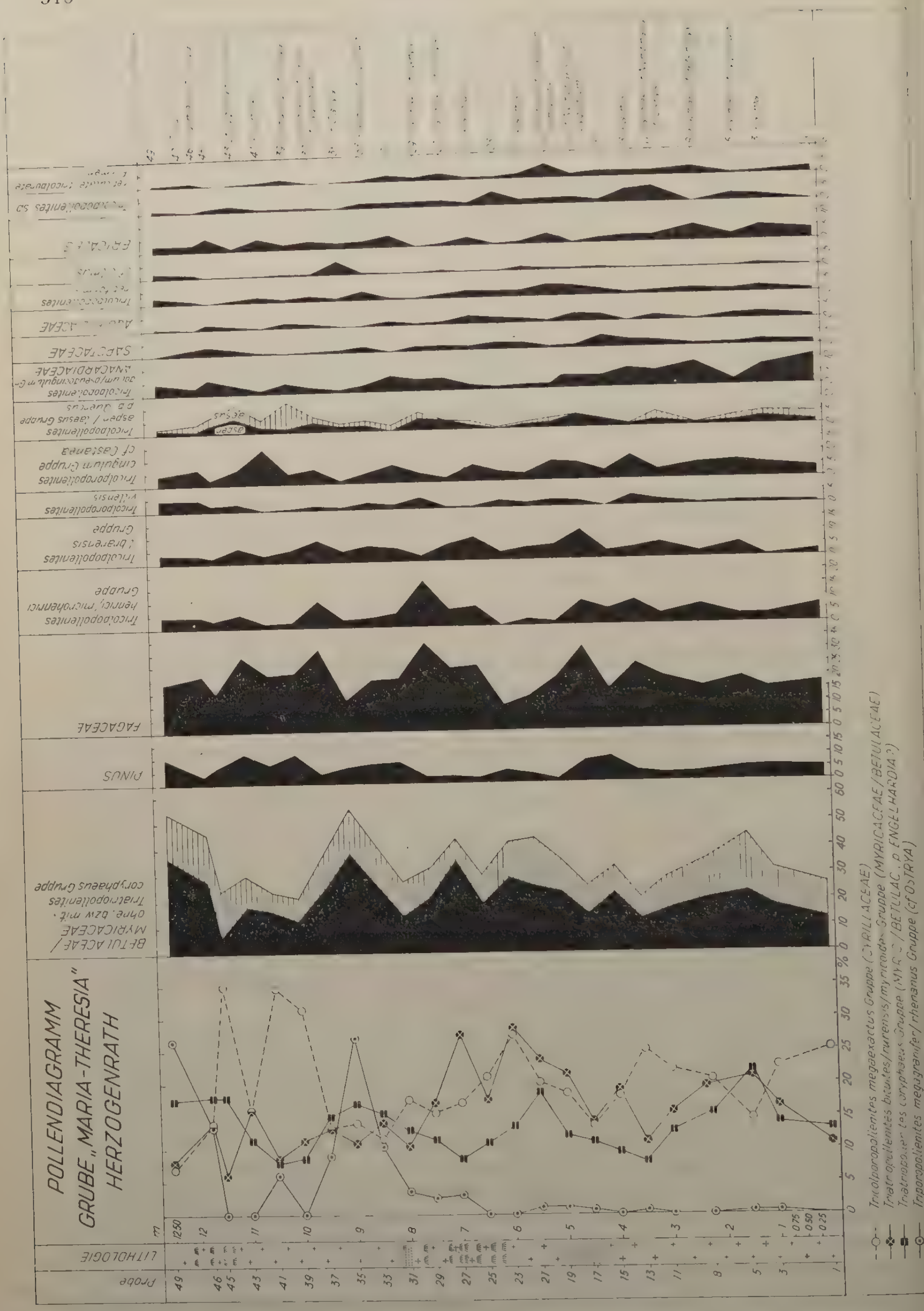
Triatriopollenites coryphaeus (R. Pot.) Pf. & Th.
Triatriopollenites bituites (R. Pot.) Pf. & Th.
Triatriopollenites rurensis Pf. & Th.
Triporopollenites megagranifer (R. Pot.) Pf. & Th.
Triporopollenites rhenanus Th.

Vereinzelt auftretende Formen derselben Familien:

Triporopollenites coryloides Pf. (cf. Corylus)
Polyvestibulopollenites verus (R. Pot.) Pf. & Th. (cf. *Alnus*)
Polyporopollenites carpinoides Pf. (cf. *Carpinus*)
Trivestibulopollenites betuloides Pf. (cf. *Betula*)
Triatriopollenites myricoides (Kremp) Pf. & Th. (? *Myricaceae*)

In Spalte 2 sind die *Betulaceae/Myricaceae* zusammen eingetragen worden. Schwarz: *Betulaceae/Myricaceae* ohne die *Triatriopollenites coryphaeus* Gruppe; waagerechte Streifung: die *T. coryphaeus*-Formen mit einbezogen. Diese Trennung wurde durchgeführt wegen der vermuteten Verwandtschaft der kleinen *T. coryphaeus*-Typen – *T. coryphaeus microcoryphaeus* (R. Pot.) Pf. & Th. – zu *Engelhardia*, welche der Familie der *Juglandaceae* angehört.

Die *Betulaceae/Myricaceae* (mit oder ohne *T. coryphaeus*) zeigen insgesamt keine grosse Schwankungen in Prozentsatz; die einzelnen Arten oder Artengruppen dieser Familien aber weisen mehr Variation in ihren Prozentsatz auf. Dementsprechend wurden in der Spalte 1 die wichtigsten Vertreter der genannten Familien in ein sogenanntes "Kompositionsdiagramm" eingetragen. Es war durchweg möglich, die Formen *Triatriopollenites rurensis*, *T. bituites* und *T. myricoides* von einander zu trennen; weil es sich aber um einander sehr nahestehende Formen handelt und die Abtrennung der einzelnen Arten immer persönlich beeinflusst wird, wurden sie in dem Diagramm in eine Gruppe zusammengefasst. Genau dasselbe gilt für die *Triporopollenites megagranifer – T. rhenanus* Gruppe. Es sei bemerkt, dass die *megagranifer*-


POLLENDIAGRAMM
GRUBE „MARIA-THERESIA"
HERZOGENRATH
BETULACEAE / MYRICACEAE ohne, bzw. mit Triatriopollenites coryphaeus Gruppe
PINUS
FAGACEAE
Tricolporopollenites henrici/microhenrici Gruppe
Tricolporopollenites liblarensis Gruppe
Tricolporopollenites villensis
Tricolporopollenites cingulum Gruppe cf Castanea
Tricolpopollenites asper / iaesus Gruppe p.p. Quercus
Tricolporopollenites pseudocingulum Gr. ANACARDIACEAE
SAPOTACEAE
ERICACEAE
LITHOLOGIE
Probe
Tricolporopollenites megaexactus Gruppe (CYRILLACEAE)
Triatriopollenites bituitus/rurensis/myricoides Gruppe (MYRICACEAE/BETULACEAE)
Triatriopollenites coryphaeus Gruppe (MYR. / BETULAC., p. ENGELHARDIA?)
Triporopollenites megagranifer/rhenanus Gruppe (cf OSTRYA)

bb.

Typen gegenüber den *rhenanus*-Typen immer weit in der Minderzahl sind. Es könnte auch noch ein Teil dieser Gruppe von manchen Autoren als zu *Triatriopollenites myricoides* gehörend aufgefasst werden; letztere unterscheidet sich jedoch durch die immer stark verfaltete Exine; ausserdem besteht in unseren Proben ein Grössenunterschied. Die *megagranifer rhenanus* Typen haben eine Grösse von 20–30 μ, die *myricoides*-Typen sind immer über 30 μ gross.

Die Kurve der *megagranifer/rhenanus* Gruppe zeigt im höheren Teil des Profils beträchtliche Schwankungen; zweimal steigt sie rasch von 0 bis fast auf 30 % an.

Wegen der vermuteten Verwandtschaft der *megagranifer/rhenanus* Typen mit den Pollen der rezenten *Ostrya* (sehe auch POTONIÉ, THOMSON und THIERGART, 1951) könnten die erwähnten Schwankungen ökologische Bedeutung haben. Die rezente *Ostrya carpinifolia* wächst in einem trockenen, ziemlich warmen Klima, hauptsächlich südlich der Alpen. Die Schwankungen in unserem Profil könnten also bedeuten, dass es während der Ablagerung des höheren Teils des Flözes zweimal zu einer beträchtlichen Umweltänderung gekommen ist. Die Häufigkeitsmaxima der cf. *Ostrya* stimmen mit der Häufigkeitsabnahme der *Cyrillaceae* überein. Letztere Familie ist vor allem an ein feuchtes Milieu gebunden. Zusammenfassend kann man also auf eine zweimal aufgetretene, rasch einsetzende und bedeutende Feuchtigkeitsabnahme schliessen. Es sei noch darauf hingewiesen, dass der Kurvenverlauf der cf. *Ostrya* ziemlich unabhängig von den übrigen *Betulaceae/Myricaceae* ist.

Betulaceae/Myricaceae sind im ganzen Profil reichlich vorhanden mit Maxima bis zu 55 %.

Cyrillaceae

Zu den *Cyrillaceae* werden gerechnet die Formart *Tricolporopollenites megaexactus* (R. Pot.) Pf. & Th. mit den Unterarten *T. megaexactus exactus* (R. Pot.) Pf. & Th. und *T. megaexactus brühlensis* (Th.) Pf. & Th. Der Unterschied der beiden Unterarten beruht auf ihrer Grösse, im Diagramm sind sie nicht getrennt worden.

Die *Cyrillaceae* treten im ganzen Profil massenhaft auf, mit Maxima bis zu 35 % (Spalte 1). Auf das Verhältnis zu den *Ostrya*-ähnlichen Typen wurde bereits hingewiesen.

Sapotaceae

Die tetracolporaten Formen, welche gut mit den Pollen der rezenten *Sapotaceae* übereinstimmen, machen in unseren Proben nie mehr als 5 % der gesamten Pollenflora aus, kommen jedoch in fast allen Proben vor (Spalte 11).

Pinaceae

In der Braunkohle der Maria Theresia fast ausschliesslich vertreten durch den *Pinus-Haploxylon*-Typus: *Pityosporites microalatus* (R. Pot.) Pf. & Th. Der *Diploxylon*-Typus: *Pityosporites labdacus* (R. Pot.) Pf. & Th. spielt in unserem Material nur eine ganz untergeordnete Rolle.

Die *Pinaceae* sind nie häufig und überschreiten stellenweise kaum 10 % (Spalte 3).

Anacardiaceae

Es werden zu den *Anacardiaceae* gerechnet die Formarten *Tricolporopollenites dolium* (R. Pot.) Pf. & Th. und *Tricolporopollenites pseudocingulum* (R. Pot.) Pf. & Th.

Im unteren Teil des Profils herrschen die rauheren und grösseren *T. dolium*-Formen vor, im oberen Teil die doppelkegelförmigen *T. pseudocingulum* Formen. Zwischen beiden Typen gibt es viele Uebergänge. Der Kurvenverlauf deutet auf eine gewisse Häufigkeitsabnahme von unten nach oben hin (Spalte 10).

Fagaceae

In Spalte 4 sind alle von uns zu den *Fagaceae* gerechneten Formen zusammengefasst; in den Spalten 5–9 sind die einzelnen Formarten oder Formartengruppen eingetragen:

Tricolpopollenites henrici (R. Pot.) Pf. & Th.
Tricolpopollenites microhenrici (R. Pot.) Pf. & Th.
Tricolpopollenites librarensis Th.
Tricolpopollenites asper Pf. & Th.
Tricolpopollenites laesus (R. Pot.) Pf. & Th.
Tricolporopollenites villensis Th.
Tricolporopollenites cingulum (R. Pot.) Pf. & Th.

Tricolpopollenites henrici und *T. microhenrici*, welche eine gewisse Verwandtschaft mit rezentem *Quercus*-Pollen zeigen, erreichen auf 7.50 M ein Maximum von 17 %; in allen anderen Proben überschreiten sie niemals 10 %.

Bei *Tricolpopollenites librarensis* konnte ein Unterschied gemacht werden zwischen den Unterarten *T. librarensis librarensis* Th. und *T. librarensis* fallax (R. Pot.) Pf. & Th. Diese glatten Formen, welche ebenfalls den Cupuliferen zugerechnet werden können, lassen sich, u.A. auf Grund der Skulptur, leicht von den *henrici*-Typen unterscheiden.

Tricolpopollenites asper und *T. laesus* sind durch viele Uebergänge mit einander verbunden; der gestreifte Anteil der Kurven in Spalte 9 entspricht dem *laesus*-Typ, der schwarze Anteil dem *asper*-Typ. Beide letztgenannte Formen stimmen unter den tertiären "*Fagaceae*" am besten mit den Pollen der rezenten Gattung *Quercus* überein.

Tricolporopollenites villensis ist in unserem Material eine der am schwersten abtrennbaren Formen; vor allem der Unterschied mit *Tricolporopollenites pseudocingulum* und den grösseren Formen der *Tricolporopollenites cingulum* Gruppe erwies sich in manchen Proben als recht schwierig, weil genannte Formen häufig durch Uebergänge mit einander verbunden sind. Auch fanden sich Uebergänge zwischen *T. villensis* und den manchmal auftretenden schwach tricolporaten Pollen der *Tricolpopollenites microhenrici*. Die von uns als *T. villensis* gedeuteten Formen machen nie mehr als 5 % der gesamten Pollenmasse aus.

Die Gruppe von *Tricolporopollenites cingulum* (Spalte 8), in der zusammengefasst sind *T. cingulum fusus* (R. Pot.) Pf. & Th., *T. cingulum pusillus* (R. Pot.) Pf. & Th. und *T. cingulum oviformis* (R. Pot.) Pf. & Th., lässt sich z. T. (beide letztgenannte Unterarten) sehr gut mit dem Pollen der rezenten Gattung *Castanae* vergleichen.

Die *Fagaceae* zeigen keine grosse Prozentsatzschwankungen und kommen regelmässig im ganzen Profil vor. Zusammen mit den *Cyrillaceae* und den *Betulaceae*/*Myricaceae* bilden sie die Hauptmasse (bis 80–90 %) des Pollenbestandes der Maria Theresia.

Aquifoliaceae

Tricolporopollenites iliacus (R. Pot.) Pf. & Th. und *Tricolporopollenites microiliacus* Pf. & Th. stimmen gut mit den Pollen der rezenten *Aquifoliaceae*, Gattung *Ilex*, überein.

Regelmässig vorkommend, aber immer weniger als 5 % (Spalte 12).

Ulmaceae

Polyporopollenites undulosus (Wolff) Pf. & Th. darf höchstwahrscheinlich mit dem Pollen der rezenten *Ulmaceae* verglichen werden. Spärlich auftretend; auf 9 M ein Häufigkeitsmaximum von 5 % (Spalte 14).

Bei einem Vergleich der Kurven von cf. *Ostrya* und den *Ulmaceae* fällt auf, dass die *Ulmaceae* immer nur dann auftreten, wenn auch die cf. *Ostrya* anwesend ist.

Ericaceae

In unserem Material hauptsächlich vertreten durch *Tetradopollenites ericius* (R. Pot.) Pf. & Th. und *Tetradopollenites callidus* (R. Pot.) Pf. & Th.

Regelmässig vorkommend; überschreiten kaum 5 % (Spalte 15).

Tricolpopollenites retiformis

Pollen der Art *Tricolpopollenites retiformis* sind in allen Proben, aber niemals häufig, anwesend (Spalte 1.3). Eine Verwandtschaft mit dem Pollen der rezenten *Platanus* und, vielleicht, teilweise mit *Salix* ist wahrscheinlich.

Taxodiaceae/*Cupressaceae*

Inaperturopollenites dubius (R. Pot. & Ven.) Pf. & Th. und *Inaperturopollenites hiatus* (R. Pot.) Pf. & Th. kommen in fast allen Proben vor, sind aber immer sehr stark korrodiert. Die mit Sicherheit zu bestimmenden Pollen dieser Arten machen nie mehr als 2 % des gesamten Pollengehaltes aus.

Tricolpopollenites sp.

Mit *Tricolpopollenites sp.* wurden kleine (15–18 μ), immer in der Polaransicht vorliegende, völlig glatte Formen mit tief eingeschnittenen Colpi bezeichnet. Es fehlt jede Skulptur. Botanische Zugehörigkeit unbekannt (Spalte 16).

Tricolporate, retikulate Formen (Spalte 17).

Derartige Pollentypen kommen in den meisten Proben, aber immer nur in sehr kleinen Zahlen vor. Es handelt sich um Formen wie *Tricolporopollenites microreticulatus* Pf. & Th. (cf. *Sambucus*?) und damit pollenmorphologisch verwandte Arten wie *Tricolporopollenites eureticulatus* Manten (cf. *Viburnum*) und *Tricolporopollenites reticulatus* Manten (*Hamamelidaceae*). In einigen Proben wurden einige, dem Pollen der rezenten *Artemisia* sehr ähnliche Pollentypen festgestellt.

Sonstige Formen

In der letzten Spalte des Diagramms sind noch, nach ihrer vermuteten botanischen Zugehörigkeit, einige Gattungen und Familien angegeben, welche nur in sehr niedrigen Zahlen, jedoch regelmässig beobachtet worden sind. Sie werden hier genannt, weil ihr Vorkommen wichtig sein kann für Rückschlüsse auf die Pflanzensoziologischen und Klimaverhältnisse (*Palmae*, *Lygodium* u.s.w.); man vergleiche auch mit dem Vorkommen der *Sapotaceae*.

EINSTUFUNG DES DIAGRAMMS

Beim Vergleichen unseres Diagramms mit den Diagrammen des Hauptflözes der Rheinischen Braunkohle in der Grube Fortuna (THOMSON, 1950, 1954) wird eine Korrelation mit der unteren Hälfte des Hauptflözes wahrscheinlich. Man beachte vor allem den Prozentanteil der *Tricolpopollenites henrici/microhenrici* Gruppe, sowie das völlig Fehlen von *Sciadopitys*-ähnlichem Pollen in unserem Material. Jedoch gibt es auch einige Unterschiede; so ist z.B. der *Taxodiaceae/Cuprassaceae* Anteil der Maria Theresia nie grösser als 2 %; im unteren Teil des Hauptflözes erreichen genannte Familien manchmal Höchstwerte von etwa 80 %. Die *Inaperturopollenites dubius* – und *I. hiatus* – Pollen sind in sunserem Material aber immer sehr schlecht erhalten; der richtige Prozentsatz könnte bedeutend mehr als 2 % sein. Diese Vermutung stimmt ganz mit vorläufigen Holzbestimmungen von van der Burgh (pers. Mitt.) überein, welche einen beträchtlichen Anteil von *Taxodiaceae/Cupressaceae* zeigen. Pollenanalytisch ist also die Braunkohle der Maria Theresia zum Morken- oder Frimmersdorf-Horizont zu rechnen; aus geologischen Gründen (Mitt. Dr. von der Brelie) wird sie zum Morken-Horizont gerechnet.

Das Pollendiagramm der Grube Anna (Haanrade, Niederlande), das von MANTEN (1958) beschrieben wurde, zeigt auffallende Ähnlichkeit mit unserem Diagramm. Manten möchte die Kohle der Anna zu Flöz F (Frimmersdorf) rechnen.

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PALAEOBOTANY OF THE MESOPHYTIC III

PLANT MICROFOSSILS FROM THE UPPER BUNTER OF HENGELO, THE NETHERLANDS

H. VISSCHER

(*Botanical Museum and Herbarium, Utrecht*)

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Abstract

The Upper Bunter palynological assemblage described includes 54 species, assigned to 29 genera. Seven genera (*Scabratisporites*, *Guttatisporites*, *Lapposisporites*, *Pseudogravisporites*, *Paralundbladispora*, *Taeniaepollenites* and *Tubantiapollenites*) and 39 species are new; three generic descriptions are emended (*Apiculatasporites*, *Colpectopollis* and *Angustisulcites*) and three new combinations are proposed. Bisaccate pollen grains average 84 %; within this group no Upper Permian elements could be demonstrated. The assemblage is compared with other European Lower and Middle Triassic assemblages; there are no close similarities to assemblages outside Europe.

1. Introduction

As a result of the accelerated development of Lower Mesophytic palynology during the last few years, even the conclusions of recent investigations may soon become obsolete.

By starting our studies in Triassic palynology we suspected the existence of important floristic differences between the European Upper Permian and Lower Triassic series. In order to prove this suspicion we had to continue and to revise the investigations carried out by Freudenthal (1964). Under the direction of Dr. W. Klaus, Vienna, we trained in recognizing Upper Permian sporae dispersae in order to be able to make comparisons with Lower Triassic assemblages. These were investigated from Upper Bunter evaporites and pelites.

The samples studied originate from the core of a drill hole situated in the exploited part of the Hengelo salt-deposits, south of the city of Hengelo in the province of Overijssel (situation: Cox 1963, Fig. 2). The boring was carried out in 1953 by the Koninklijke Nederlandsche Zoutindustrie (Royal Dutch Salt Industry) in behalf of the construction of well 31 (situation: Cox 1963, Figs. 4, 5). In this paper it will be indicated as "Boring 31, K.N.Z., Hengelo". The investigations were performed in the Palaebotanical laboratories of the Botanical Museum and Herbarium of the State University, Utrecht, under the direction of Dr. F. P. Jonker, professor of Special Botany.

2. Conclusions

In a large part of Europe the Upper Permian sediments contain similar palynological assemblages. Apart from local differences the microfloras are identical both in the German Basin and in the Alpine regions.

This phenomenon can also be observed in the Upper Bunter. However, the microflora has changed into a totally new composition. Important Upper Permian elements like *Nuskoisporites dulhuntyi*, *Lueckisporites virkkiae*, *Falcisporites zapfei*, *Limitisporites rectus*, *Klausipollenites schaubergeri*, etc. have given way to *Triadispora* spec. div., *Voltziaceaesporites heteromorpha*, *Angustisulcites klausii*, *Alisporites grauvogeli*, etc. The regional similarities in the European (micro)flora during the Permian and Triassic periods indicate the existence of an important palaeo-phytogeographic unit. This may be of great interest for the knowledge about the Post-Carboniferous evolution of European palaeogeography. Up till now the available palynological data from Bunter sediments have been insufficient to introduce conceptions about the regional stratigraphical problems in this series.

The author was also unable to solve the local stratigraphical problem of the boundary between the Bunter and Muschelkalk; however, it is hoped that this investigation will contribute to the knowledge of the European Lower Triassic, which, until recently, remained undiscovered by palynology.

3. GEOLOGY

3.1. *General*

For a summary of the geological history and the tectonical relations in the eastern Netherlands we refer to PANNEKOEK *et al.* (1956), FABER (1960) and HAANSTRA (1963). Local geological data concerning the Hengelo region were published by COX (1963). He also summarized the historical, technical and economical aspects of salt production in the Netherlands.

The Hengelo salt-deposits are situated in the eastern part of the East Netherlands Triassic Swell, a tectonical unit extending in NW-SE direction from Eastern Flevoland in the former Zuiderzee to the Dutch-German border (PANNEKOEK *et al.* 1956, Fig. 2; HAANSTRA, 1963, Fig. 13). This unit consists mainly of Bunter (Buntsandstein) sediments with locally some remains of Muschelkalk and Liassic. These sediments are unconformably covered by Tertiary and Quaternary sands, sandy clays, gravels and peats. The eastern part of the unit is bounded by a zone of Lower Cretaceous, east of which we find the Münster Basin (PANNEKOEK *et al.* 1956, Fig. 17; FABER 1960, Fig. 175).

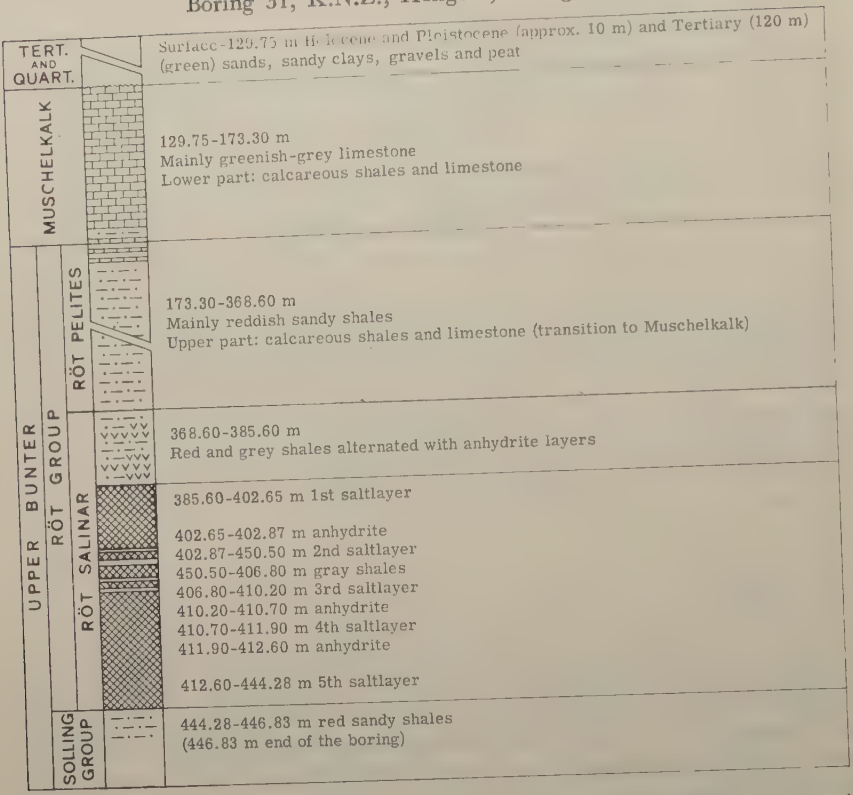
3.2. *The Bunter*

The Bunter is considered to be a lithostratigraphical series.

Besides the general geological publications by PANNEKOEK *et al.* (1956), FABER (1960) and HAANSTRA (1963) one has to take resource to the more detailed research in the German area. BOIGK (1959) and TRUSHEIM (1963) have tried to build up a lithostratigraphical classification of the Bunter. Also the eastern Netherlands have been covered by their studies. The same applies to the sedimentological approach by SINDOWSKI (1957).

TABLE 1

Boring 31, K.N.Z., Hengelo; stratigraphy



TERT. AND QUART.			Surface-129.75 m Holocene and Pleistocene (approx. 10 m) and Tertiary (120 m) (green) sands, sandy clays, gravels and peat
MUSCHELKALK			129.75-173.30 m Mainly greenish-grey limestone Lower part: calcareous shales and limestone
UPPER BUNTER	RÖT GROUP	RÖT PELITES	173.30-368.60 m Mainly reddish sandy shales Upper part: calcareous shales and limestone (transition to Muschelkalk)
		RÖT SALINAR	368.60-385.60 m Red and grey shales alternated with anhydrite layers
			385.60-402.65 m 1st saltlayer 402.65-402.87 m anhydrite 402.87-450.50 m 2nd saltlayer 450.50-406.80 m gray shales 406.80-410.20 m 3rd saltlayer 410.20-410.70 m anhydrite 410.70-411.90 m 4th saltlayer 411.90-412.60 m anhydrite 412.60-444.28 m 5th saltlayer
	SOLLING GROUP		444.28-446.83 m red sandy shales (446.83 m end of the boring)

In a great part of the Netherlands the Bunter appeared to exist in the subsoil. However, important variations in thickness have been proved (FABER 1960, fig. 91). The coarse of the isopaches in Western Germany has been shown by TRUSHEIM (1963, fig. 1). In the area of the East Netherlands Triassic Swell the thickness of the Bunter increases in SE direction. Near Hengelo the sediments amount to 900 m.

The Bunter is subdivided into the Lower-, Middle- and Upper Bunter. There is no unanimity about the limits of these subdivisions (TRUSHEIM 1963). As the samples investigated have been taken from the Upper Bunter and the Lower Muschelkalk it seems useful to treat briefly the problems about the boundaries between Middle Bunter and Upper Bunter and between Upper Bunter and Muschelkalk. In the Netherlands one usually starts the Upper Bunter with the Röt salt deposits. Also BOIGK (1959) takes this view with regard to his subdivision of the German Bunter. The Röt is considered identical with the Upper Bunter and can be divided into the Röt salinar and the younger Röt pelites. The underlying Solling Group belongs to the Middle Bunter. Another boundary has been proposed by TRUSHEIM (1963). Both the Solling and the Röt belong to the Upper Bunter; so the latter cannot be considered identical with the Röt. The boundary between the upper part of the Middle Bunter, the Hardegsen Group, and the Solling Group is marked by an uncomformity ("H-Diskordanz") whose occurrence has been demonstrated from the Dutch-German border up to Thüringen and which can be correlated with the well-known fossil land surface in southern Germany. It may be regarded as the most important hiatus within the Bunter, if not within the whole German Triassic (TRUSHEIM 1963, figs. 2, 8). Because of the comparatively small regional extension of the Röt salinar we prefer the "H-Diskordanz" as a criterion for the boundary between the Middle Bunter and the Upper Bunter. Unlike the interpretation by the K.N.Z. we consider the red sandy shales underlying the salt deposits to be the Upper Bunter (Solling Group; compare Table 1).

Though the upper part of the Röt pelites may already be calcareous and dolomitic, the base of the German Muschelkalk is characterized by a yellowish crystalline limestone layer, often developed as a conglomerate. This layer starts the so-called Wellenkalk facies (Boigk 1959). In the eastern Netherlands, however, the boundary between the Bunter- and the Muschelkalk series cannot be drawn with the same accuracy. Usually the differences in colour of the calcareous shales will settle the matter; the Röt is brownish, the Muschelkalk greyish (Faber 1960).

In the stratigraphical section (Table 1) the boundary between the Upper Bunter and Muschelkalk has been copied from the interpretation by the K.N.Z., though outstanding lithological differences could not be demonstrated.

4. Preparation and study technique

Apart from some experiments with other techniques the sample-digestion technique employed in preparing the samples has been as follows:

The samples were pulverized. Depending on the presence of NaCl or $CaCO_3$ the powder was boiled in water or treated with diluted HCl respectively. The residue was placed in a 45 % HF solution for 24–48 hours. In some cases treatments with HCl were added to stimulate the solubility of the SiO_2. The effect of the HF was hampered by a film of fluor silicates around the SiO_2 particles. HCl dissolved the fluor silicates. Also, after the HF treatment a wash with HCl i. to follow. Since many samples appeared to contain a great deal of anhydrite or gypsum it was necessary to practice gravity separations For this separation a solution of ZnBr in 10 % HCl was used.

For counting microscopic slides were made from the concentrated fossil preparations, using glycerine. In order to study and describe the various species we used single grain slides made according to the preparation method of Punt (1962) which are numbered 31-HV-01, 31-HV-02, etc. They are stored in the Palaeobotanical laboratories of the Botanical Museum and Herbarium of the State University, Utrecht, the Netherlands.

5. Quantitative palynology

5.1. *Presence of sporae dispersae*

We have investigated 43 core-samples from the boring 31, K.N.Z., Hengelo; they originate both from the Upper Bunter and the Lower Muschelkalk sediments (Table 2). In the latter no pollen and spores could be indicated (samples 1–6). Neither did the reddish Fe^{3+}-containing layers yield any microflora. The calcareous shale of sample 8 and the greyish sandy shales of samples 17, 20 and 26 contained some badly conserved pollen grains and spores. This also applies to the greyish shales of the upper part of the Röt salinar (samples 31 and 33). Five salt layers more or less mixed with clay and anhydrite can be distinguished (Table 1). They contain sporae dispersae in

TABLE 2

Stratigraphical position of the samples and occurrence of sporae dispersae (+)

sample number	depth below surface (m)	stratigraphical position	sporae disp.
1	152.32	Muschelkalk	
2	161.76	Muschelkalk	
3	166.69	Muschelkalk	
4	167.73	Muschelkalk	
5	170.05	Muschelkalk	
6	172.36	Muschelkalk	
7	175.85	Röt pelites (calcareous)	
8	177.76	Röt pelites (calcareous)	+
9	184.50	Röt pelites (calcareous)	
10	197.46	Röt pelites (red shales)	
11	212.45	Röt pelites (red shales)	
12	230.15	Röt pelites (red shales)	
13	242.19	Röt pelites (red shales)	
14	251.63	Röt pelites (red shales)	
15	261.52	Röt pelites (red shales)	
16	266.35	Röt pelites (red shales)	
17	271.33	Röt pelites (grey shales)	+
18	286.07	Röt pelites (red shales)	
19	301.90	Röt pelites (red shales)	
20	307.21	Röt pelites (grey shales)	+
21	312.52	Röt pelites (red shales)	
22	322.25	Röt pelites (red shales)	
23	330.41	Röt pelites (red shales)	
24	335.93	Röt pelites (red shales)	
25	339.90	Röt pelites (red shales)	
26	347.52	Röt pelites (grey shales)	+
27	353.89	Röt pelites (red shales)	
28	359.95	Röt pelites (red shales)	
29	364.85	Röt pelites (red shales)	
30	366.93	Röt pelites (red shales)	
31	372.83	Upper Röt salinar	+
32	276.78	Upper Röt salinar	
33	382.85	Upper Röt salinar	+
34	392.00	1st salt layer	+
35	399.40	1st salt layer	+
36	404.00	2nd salt layer	+
37	405.50	2nd salt layer/shales	+
38	406.80	shales/3rd salt layer	+
39	411.50	4th salt layer	+
40	431.85	5th salt layer	+
41	439.47	5th salt layer	+
42	444.28	5th salt layer/Solling Gr.	
43	446.78	Solling Group	

widely varying numbers. The shales between 405.50 and 406.80 m yielded the richest preparations. The red Solling sediments are sterile.

In general the Röt pollen is badly preserved. A sufficient number of rather well-preserved pollen grains, necessary for studying and describing the species, has been found only in the relatively rich preparations. Unlike the pollen, the spores are usually well preserved. They always occur in very low percentages.

5.2. *The Hengelo palynological assemblage*

The quantitative analysis has been based on the 54 formspecies described in this paper.

The qualitative distribution of these species within the various pollen and spores bearing samples is shown in Table 3a.

Very few samples appeared to contain well preserved specimens, which is essential to detailed counting. Sample 37 turned out to contain a relatively rich microflora. Table 3b reproduces a counting based on this sample. In order to obtain the many low percentages it has been necessary to choose a high pollen sum (= 1000 determinable pollen grains and spores). On account of our observations we believe the percentages of this sample to be representative for the entire Röt salinar. The many gaps in Table 3a are due to the relatively smaller number of determinable pollen grains and spores.

It has been impossible to establish whether the percentages of Table 3b also apply to the samples 17, 20 and 26, which were taken from the Röt pelites. However, the percentages of sample 37 do certainly not apply to the microflora from the calcareous shale of sample 8 (upper part of the Röt pelites, transition to the Lower Muschelkalk). Here too we are dealing with a very poor and badly preserved microflora; however, a counting is reproduced in order to get an impression of the changed percentages (Table 3c).

6. COMPARATIVE PALYNOLOGY

6.1. *Comparisons within the section investigated*

As no important microfloristic changes were demonstrated within the Röt salinar it is sufficient to discuss the differences between Röt salinar and Röt pelites. A comparison of the percentages of sample 8 (calcareous shale in the upper Röt pelites) with the percentages of sample 37 (representative for the Röt salinar) reveal some striking differences (Table 3b, c):

increased percentages of
  Paralundbladispora quadriiuga
  Paralundbladispora vieta
  Saturnisporites praevius
  Alisporites grauvogeli
  Colpectopollis ellipsoideus
  Microcachryidites doubingeri
  Angustisulcites klausii
decreased percentages of
  Voltziaceaesporites heteromorpha
  Triadispora crassa

The different character of sample 8 is specially owing to the increased percentage of *Angustisulcites klausii* at the cost of *Voltziaceaesporites heteromorpha* and *Triadispora crassa*.

In view of the very poor data obtained from the samples 17, 20

TABLE 3

Qualitative distribution of sporae dispersae in the various samples and quantitative analysis o samples 37 (Röt salinar) and 8 (Upper Röt pelites; transition to Muschelkalk)

Species	a Qualitative Distribution 8	17	20	26	31	33	34	35	36	37	38	39	40	41	b mean % 37	c mea 8
Calamaspora sp.							+								—	
Psilatriletes triassicus										+	+				0.4	
Apiculatasporites plicatus	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1.2	3
Scabratisporites scabratus							+		+	+	+	+		+	0.2	
Verrucosisporites jenensis							+	+	+	+	+			+	0.4	
Verrucosisporites reinhardtii							+	+	+	+	+	+		+	0.3	
Verrucosisporites pseudomorulae						+	+			+	+	+			0.4	
Guttatisporites guttatus						+	+		+	+	+				0.4	
Guttatisporites elegans										+	+				0.2	
Guttatisporites microechinatus							+			+	+			+	0.4	
Lapposisporites lapposus							+		+	+				+	0.2	
Lapposisporites villosus							+			+					0.2	
Lapposisporites armatus										+					0.2	
Lapposisporites loricatus							+			+					0.2	
Densoisporites caretteae							+			+	+	+	+		0.4	
Pseudogravisporites reticulatus										+	+				0.3	
Anguisporites tenuis					+		+		+	+				+	0.5	
Paralundbladispora quadriiuga	+		+				+			+	+			+	0.3	
Paralundbladispora vieta	+		+				+			+	+				0.2	
Kraeuselisporites hystrix						+	+	+	+	+	+	+			0.4	
Kraeuselisporites hoofddijkensis	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0.8	
Saturnisporites praevius	+		+				+		+	+	+				0.2	
Nuskoisporites inopinatus										+	+				0.4	
Voltziaceaesporites heteromorpha	+	+	+	+	+	+	+	+	+	+	+	+	+	+	21.0	1
Alisporites microreticulatus						+	+	+	+	+	+	+		+	0.7	
Alisporites grauvogeli	+	+	+	+	+	+	+	+	+	+	+	+	+	+	6.7	1
Colpectopollis ellipsoideus	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1.8	
Chordasporites voltziaformis	+						+		+	+	+	+			0.5	
Falcisporites snopkovae							+		+	+	+	+		+	1.2	
Paravesicaspora planderovae							+		+	+	+	+	+	+	2.0	
Microcachryidites doubingeri	+						+		+	+	+				0.4	
Triadispora crassa	+	+	+	+	+	+	+	+	+	+	+	+	+	+	18.4	
Triadispora staplini					+	+	+	+	+	+	+	+	+	+	0.9	
Triadispora falcata							+			+	+				0.2	
Triadispora muelleri	+						+		+	+	+				0.3	
Triadispora plicata							+	+	+	+	+	+	+		0.5	
Triadispora epigona	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1.8	
Illinites trivisus										+	+				1.4	
Angustisulcites klausii	+	+	+	+	+	+	+	+	+	+	+	+	+	+	6.3	
Angustisulcites grandis							+		+	+	+	+	+	+	2.1	
Angustisulcites gorpii							+	+	+	+	+	+	+	+	3.5	
Lunatisporites puntii							+		+	+				+	1.0	
Striatoabietites aytugii	+				+		+		+	+	+	+		+	2.1	
Taeniaepollenites jonkeri							+	+	+	+	+	+	+	+	1.8	
Taeniaepollenites multiplex	+			+	+	+	+	+	+	+	+	+	+	+	4.1	
Taeniaepollenites discrepans							+		+	+	+	+			1.4	
Taeniaepollenites hengeloensis							+		+	+	+	+			0.7	
Tubantiapollenites striatitoides						+	+		+	+	+				0.7	
Tubantiapollenites balmei	+						+	+	+	+	+	+	+	+	1.3	
Tubantiapollenites schulzii							+	+	+	+	+	+	+	+	1.4	
Cycadopites coxii				+	+		+	+	+	+	+	+	+	+	3.0	
Cycadopites sufflavus					+	+	+	+	+	+	+	+	+	+	2.5	
Cycadopites trusheimii							+			+	+	+			0.7	
Cycadopites crenulatus							+	+	+	+	+	+		+	1.4	

and 22 it has been impossible to check whether this change is sudden or gradual.

6.2. *Comparisons with Boring 69, K.N.Z., Hengelo*

The palynological investigations in the Dutch Röt salinar were started by FREUDENTHAL (1964). He studied samples from another K.N.Z. drill hole (69). The average quantitative distribution of sporae dispersae in the Röt, as given by Freudenthal, is reproduced in Table 4.

By far the greatest part of the Röt microflora was supposed to consist of components that play already a more or less important part in the European Upper Permian (group 1). We have to refute this concept with emphasis; the presence of Upper Permian saccate pollen could be demonstrated neither in Freudenthal's slides nor in our own preparations.

TABLE 4

Quantitative distribution of pollen species and spores in the assemblage from Boring 69, K.N.Z., Hengelo (modified after FREUDENTHAL 1964, t. 1)

species	mean (%)
Group 1. Species based on a holotype from the European Upper Permian	
Eridospollenites bentzi	0.2
Eridospollenites parvus	4.1
Jugasporites delasaucei	2.6
Jugasporites moersensis	0.5
Klausipollenites schaubergeri	7.4
Falcisporites zapfei	27.0
Platysaccus papillionis	2.0
Labiisporites granulatus	28.3
Favisporites tenuis	7.4
Taeniaesporites noviaulensis	5.0
Taeniaesporites nubilis	?
Striatites richteri	0.5
Group 2. Species based on a holotype from the Canadian Lower Triassic	
Falcisporites staplini	3.0
Group 3. Species based on a holotype from the European Upper Triassic	
Pityosporites devolvens	7.7
Group 4. Species based on a holotype from the assemblage investigated	
Falcisporites triangularis	0.3
Falcisporites ? grandis	0.3
Platysaccus hengeloensis	0.6
Angustisulcites klausii	0.5
Protosacculina jansonii	1.3
Group 5. *Sporites*	1.0

Also the presence of group 2 and group 3 in the Röt salinar is rather unlikely (*Falcisporites staplini* unequals *Triadispora staplini*).

Considering the species described by Freudenthal (group 4) only *Falcisporites*? *grandis* (≡ *Angustisulcites grandis*) and *Angustisulcites klausii* could be maintained. Our concepts with regard to the systematical positions of Freudenthal's species will be discussed in the systematical part of this paper.

Even after a "systematical revision" it has not been possible to compare Freudenthal's data with the results of our investigations. However, we are of opinion that there are no appreciable differences between the spectra of the two borings.

The ratio between striate pollen and non-striate pollen in the counting of sample 37 (approx. 1 : 2) differs from the ratio mentioned by Freudenthal (8 : 91). Besides considering *Illinites* and *Angustisulcites* as striate pollen, this difference is attributable to the higher pollen sum. This may also explain the more prominent percentages of *Sporites*.

6.3. *Comparisons with other European Bunter and Muschelkalk assemblages*

Similarities to Lower Triassic palynological assemblages outside Europe, for example Canada (Jansonius 1962) and Australia (Balme 1963), can only be found at a generic level. So comparisons can be restricted to some European assemblages.

Klaus (1964) investigated the characteristic microflora of German and French Upper Bunter sediments and also that of the Alpine Upper "Werfener Schichten", which can be correlated with the Upper Bunter. He also studied samples from German, French and Italian Middle Muschelkalk.

Finding characteristic assemblages in Upper Permian, Upper Bunter, Middle Muschelkalk and Keuper, Klaus states that sediments of these series can be distinguished palynologically.

Table 5 shows a comparison with the Bunter and Muschelkalk assemblages described by Klaus (1964). Three groups of species can be distinguished:

1. Species occurring both in the Upper Bunter (possibly also in the Middle Muschelkalk) studied by Klaus and in the Hengelo Röt group. The regional distribution of these species appears to include the eastern Netherlands.
2. Species occurring in the Middle Muschelkalk studied by Klaus but also in the Upper Bunter of Hengelo. In this group only *Microcachryidites doubingeri* shows an increased percentage in the upper part of the Röt pelites (sample 8), which may be interpreted as a Muschelkalk "influence".
3. Species recognized in Upper Bunter and/or Middle Muschelkalk samples from Germany, Austria, France and Italy but unknown from the Hengelo Röt sediments.

Klaus states that *Voltziaceaesporites heteromorpha* decreases in the Muschelkalk series. This view is supported by the diminished per-

TABLE 5

Qualitative comparison with the assemblages investgated by KLAUS (1964)

species	Klaus 1964		boring 31	
	Bunter	Musch.	37	8
Group 1.				
Triadispora staplini	+		+	
Triadispora falcata	+		+	
Triadispora crassa	+		+	+
Illinites melanocorpus ¹)	+	+	+	+
Voltziaceaesporites heteromorpha	+	+	+	+
Alisporites grauvogeli	+		+	+
Group 2.				
Triadispora plicata		+	+	
Triadispora epigona		+	+	+
Striatoabietites balmei ²)		+	+	+
Microcachryidites doubingeri		+	+	+
Group 3.				
Jugasporites renalis		+		
Jugasporites commilvinus	+			
Illinites kosankei	+			
Illinites chitinoides		+		
Taeniaesporites novimundi		+		
Taeniaesporites austriacus	+			
Voltziaceaesporites nephrosaccus	+	+		
Sulcosaccospora minuta		+		
Alisporites progrediens		+		
Chordasporites magnus	+			
Chordasporites cf. *singulichorda*		+		
Microcachryidites fastidioides	+			
Microcachryidites sittleri	+			
Tsugaepollenites oriens		+		

¹) probably identical with *Angustsulcites klausii.*
²) identical with *Tubantiapollenites balmei.*

centage of this species in the upper part of the Röt pelites (sample 8). It is of great interest to compare the quantitative distribution of the species of *Triadispora* (Table 6):

TABLE 6

Quantitative distribution of species of Triadispora within the assemblages investigated by KLAUS (1964) and the Hengelo Röt salinar

species	Klaus 1964		Hengelo Röt sal.
	Bunter	Musch.	
Triadispora crassa	+ +		+ + +
Triadispora staplini	+ + +		+
Triadispora falcata	?		+
Triadispora epigona		+ +	+
Triadispora plicata		+ +	+

percentages: + + + high; + + moderate; + low.

Triadispora crassa exists both in the Bunter studied by Klaus and in our preparations. It is a rather dominant species.

Triadispora staplini is even more frequent in Klaus' samples. In the Hengelo Röt, however, it is fairly uncommon.

Klaus does not mention the avarage of *Triadispora falcata*, known from the Upper Bunter. In the Hengelo assemblage this species is very rare.

Triadispora epigona and *Triadispora plicata* are important elements of the Middle Muschelkalk assemblages from Kochendorf (Germany), Sarralbe (France) and Recoaro (Italy). However, they also exist in low percentages in the Hengelo Röt Group.

Considering the existence of progressive transitions in the *Triadispora*-group – at least in the Hengelo assemblage – these species may originate from the same conifer species. But in this case the differences in quantitative distribution are still more striking, and besides biostratigraphical and palaeo-phytogeographical aspects one has to reckon with phylogenetic considerations (compare p. 350).

REINHARDT (1964a, b) described some species from the Lower Röt of Thüringen. The following elements of this incomplete assemblage can also be found in the Hengelo Röt:

Verrucosisporites jenensis
Alisporites microreticulatus
Nuskoisporites muelleri (≡ *Triadispora muelleri*)

There are no resemblances to the Middle Bunter microflora described by SCHULZ (1964). In future palynology may provide the possibilities to demonstrate the important "H-Discordanz" (p. 318) between Middle and Upper Bunter biostratigraphically.

7. DESCRIPTIVE PALYNOLOGY

ANTETURMA *Sporites* H. Potonié 1893
TURMA *Triletes* (Reinsch 1881) Potonié & Kremp 1954
SUBTURMA *Azonotriletes* Luber 1935
INFRATURMA *Laevigati* (Bennie & Kidston 1886) Potonié 1956

Calamaspora Schopf, Wilson & Bentall 1944

Type species: *Calamaspora hartungiana* Schopf 1944 in SCHOPF, WILSON and BENTALL 1944, p. 51, f. 1.

Calamaspora sp.
Fig. 1; Plate VI, Fig. 2.

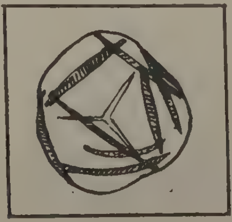


Fig. 1. *Calamaspora* sp.

Remarks and comparisons: Some spores considered as *Calamaspora* have been found in sample 34. Because of the few specimens found and the bad preservation it has been impossible to compare our forms with the numerous species of *Calamaspora* mentioned in the palynological literature. *Calamaspora* sp. possesses an irrigular, but fundamentally circular outline; diameter approx. 60 μ. Exine smooth with fine infrastructure; thickness approx. 1 μ. Length of the Y-mark rays approx. 4/5 of the spore radius; usually the sutures are widely opened. Strongly folded. *Calamaspora* sp. differs from *Calamaspora nathorstii* (Halle 1906) Klaus 1960, which is important to Upper Triassic and Lower Jurassic stratigraphy, by its bigger size and its thicker exine.

Psilatriletes (van der Hammen 1954) ex Potonié 1956

Type species: *Psilatriletes* (al. *Punctatisporites*) *detortus* (Weyland & Krieger 1953) Potonié 1965; WEYLAND and KRIEGER 1953, t. 14, f. 24.

Psilatriletes triassicus n. sp.
Fig. 2; Plate VI, Fig. 5.

Holotype: *Psilatriletes triassicus* n. sp.
Single grain side 31-HV-276: plate VI, Fig. 5.

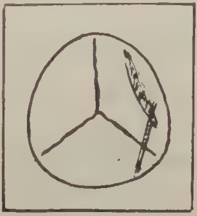


Fig. 2. *Psilatriletes triassicus*

Diagnosis: Spores trilete, azonal, with convex-triangular equator; diameter holotype 46 μ. Smooth exine with fine infrastructure; thickness approx. 1.5 μ. Faintly wavy trilete rays extend to equator. Strongly folded, due to compression.

Remarks and comparisons: On account of the strongly convex-triangular outline we consider our forms as *Psilatriletes* (van der Hammen 1954) ex Potonié 1956 (*Psilatriletes* van der Hammen 1956b seems to be unvalid; compare POTONIÉ 1960, p. 20). Unlike species of the genera *Leiotriletes* Naumova 1937 emend. Potonié & Kremp 1954 and *Deltoidospora* Miner 1935 emend. Potonié 1956 (syn. *Deltoidisporites* Danzé-Corsin & Laveine 1963), *Psilatriletes triassicus* does not include forms with straight or concave-triangular sides.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar)
Occurrence: Only recognized in the shales between 405.50 and 406.80 m; rare.

INFRATURMA *Apiculati* (Bennie & Kidston 1886) Potonié 1956
SUBINFRATURMA *Nodati* Dybová & Jachowicz 1957

Apiculatasporites Ibrahim 1933 emend.

Type species: *Apiculatasporites* (al. *Sporonites*) *spinulistratus* (Loose 1932) Ibrahim 1933; POTONIÉ, IBRAHIM and LOOSE 1932, t. 18, f. 47; photo after type in POTONIÉ and KREMP 1955, t. 14, f. 214.

Diagnosis: Spores trilete, azonal, with approx. circular equator. Exine ornamentated with more or less regularly placed tapering or rather blunt echinae; height 0.5–1.5 μ. The trilete rays are often indistinct and invisible by folding; they do not extend to the equator.

Remarks and comparisons: By describing *Apiculatasporites* IBRAHIM (1933) has chosen a trilete type species. Consequently afterwards this type species has been placed in trilete genera, viz. *Apiculatisporites* (by LOOSE 1934), *Punctatisporites* (by SCHOPF, WILSON and BENTALL 1944), *Spinososporites* (by KNOX 1950) and *Planisporites* (by POTONIÉ and KREMP 1955). However *Apiculatisporites* includes megaspores (compare POTONIÉ 1956, p. 30); the usage of American authors considering apiculate forms to *Punctatisporites* is objectionable; the position of *Spinososporites* is discussed by POTONIÉ (1958, p. 21); the latter author also dealt with the relation *Apiculatasporites–Planisporites* (POTONIÉ 1960, p. 21). Yet LESCHIK (1956a) considers *Apiculatasporites* alete; because of the trilete type species this is not permissible. *Apiculatasporites* can be distinguished from *Scrabratisporites* n. gen. by its higher exinal elements (>0,5 μ).

Apiculatasporites plicatus n. sp.

Fig. 3; Plate III, Fig. 3.

Holotype: *Apiculatasporites plicatus* n.sp. Single grain slide 31-HV-109; Plate III Fig. 3.

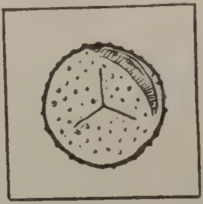


Fig. 3. *Apiculatasporites plicatus*

Diagnosis: Spores trilete, azonal, with approx. circular equator; diameter 55–65 μ (holotype 61 μ). Exine, 1.5–2 μ thick, with a rather regular but not very dense ornamentation of small echinae (basis diameter 1–2 μ, height max. 1 μ). Trilete rays approx. 2/3 of spore radius, accompanied by indistinct labra (2.5–3 μ). Usually many compression folds.

Remarks and comparisons: Because of the strong folding the Y-mark is only occasionally recognizable. The holotype of *A. plicatus*, however, shows a rather distinct Y-mark. *Apiculatasporites spinulistratus* (Loose 1932) Ibrahim 1933 differs by the more densely placed echinae of which the height exceeds the diameter.

Scabratisporites scabratus n. sp. possesses elements 0.5 μ.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 392 m (Röt salinar).

Occurrence: Most dominant spore in the Röt Group of Hengelo; yet not occurring in high percentages.

Scabratisporites n. gen.

Type species: *Scabratisporites scabratus* n.sp., Plate V, Fig. 4.

Diagnosis: Spores trilete, azonal, with approx. circular equator. Exine ornamentated with more or less regularly distributed scabrae. Trilete rays not extending to equator. Usually folded.

Remarks and comparisons: Following STRAKA (1964, Fig. 16), we define scabrae as exinal elements with a height < 0.5 μ. VAN DER HAMMEN (1954, 1956a) proposed the genus *Scabratriletes* to include scabrate, trilete microspores. POTONIÉ (1956) legitimated this name but at present *Scabratriletes* (van der Hammen 1954) ex Potonié 1956 includes megaspores with elements up to 50 μ. *Apiculatasporites* Ibrahim 1933 emend. possesses elements > 0.5 μ. The same applies to to *Planisporites* Knox 1950 emend. Potonié 1960. Moreover the latter genus possesses a subtriangular equator. At first sight *Scabratisporites* seems to have a rather smooth exine but with high magnification the scabra are visible. By these minute elements *Scabratisporites* can be distinguished from laevigate genera like *Punctatisporites* Ibrahim 1933 emend. Potonié & Kremp 1954, *Orbella* Malavkina 1949, *Phyllothecotriletes* Luber 1955 and *Cyclinasporites* Nilsson 1958. *Mariattisporites scabratus* Couper 1958 is monolete.

Scabratisporites scabratus n. sp.

Fig. 4; Plate V, Fig. 4.

Holotype: *Scabratisporites scabratus* n. sp. Single grain slide 31-HV-56; Plate V, Fig. 4.

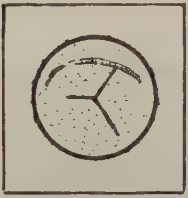


Fig. 4. *Scabratisporites scabratus*

Diagnosis: Spores trilete, azonal, with approx. circular equator; diameter 44–50 μ (holotype 48 μ). Exine 1.5–2 μ in thickness, rather regularly ornamentated with scabrae which have the shape of coni. Trilete rays of unequal length, the longest ray never exceeds 3/4 of the spores radius.

Remarks and comparisons: The spores are mostly folded. *S. scabratus* differs from *Apiculatasporites plicatus* n. sp. by its smaller exinal elements.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).

Occurrence: Röt salinar of Hengelo; rare.

INFRATURMA *Verrucati* Dybová & Jachowicz 1957

Remarks: A boundary between the subinfraturma *Verrucati* and the infraturma *Murornati* Potonié & Kremp 1954 cannot be drawn with accuracy. For example, the bigger verruca-like elements of *Guttatisporites* n. gen. seem to have developed by the growing together of some small elements. The general impression, however, remains verrucate. So we will give up the idea of considering such forms as *Murornati*, because within this infraturma the phenomenon of elements grown together is much more striking.

Verrucosisporites Ibrahim 1933 emend. Smith et al. 1964

Type species: *Verrucosisporites* (al. *Sporites*) *verrucosus* (Ibrahim 1932) Ibrahim 1933; Potonié, Ibrahim and Loose 1932, t. 15, f. 17; photo after the type in Potonié and Kremp 1955, t. 13, f. 196 and in Smith, Butterworth, Knox and Love 1964, t. 3, f. 7.

Verrucosisporites jenensis Reinhardt & Schmitz in Reinhardt 1964. Fig. 5b; Plate I, Figs. 1, 2.

Holotype: *Verrucosisporites jenensis* Reinhardt & Schmitz in Reinhardt 1964, t. 1, f. 7.

Remarks and comparisons: Our specimens well correspond to the specific description by Reinhardt (1964b). An average of 50 verrucae can be counted on the spore outline; diametrically an average of 20. *V. jenensis* differs from *Verrucosisporites reinhardtii* n. sp. by possessing a thinner exine (respectively 3–4 μ and 6–7 μ).

Occurrence: Röt salinar of Hengelo; rare. Reinhardt mentions the species from the Lower Röt of Thüringen (Germany).

Verrucosisporites reinhardtii n. sp.

Fig. 5a; Plate I, Fig. 3.

Holotype: *Verrucosisporites reinhardtii* n. sp. Single grain slide 31-HV-150; plate I, Fig. 3.

Derivatio nominis: P. Reinhardt, Geologisches Institut der Bergakademie Freiberg, Germany.

Diagnosis: Spores trilete, azonal, with covex-subtriangular equator. Very thick exine (6–7 μ), with a dense ornamentation of polygonal verrucae (diameter 2.5–5 μ, height 1.5–2.5 μ; the bigger elements only at the distal surface). An average of 37 verrucae can be counted on the spore outline, diametrically about 15–20. Between the verrucae a polygonal negative reticulum is visible. Trilete rays of the distinct Y-mark extend to 2/3–3/4 of the spore radius. Known size range 65–72 μ (holotype 67 μ).

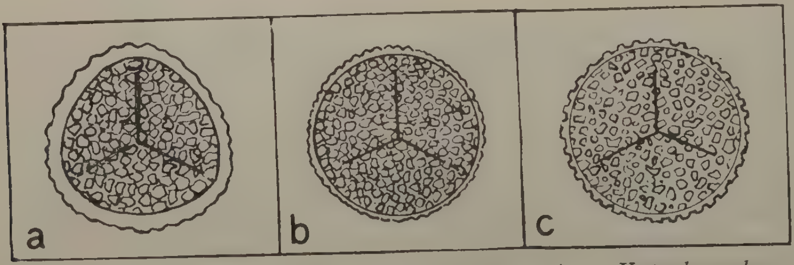


Fig. 5. *Verrucosisporites*. a. *V. reinhardtii*; b. *V. jenensis*; c. *V. psedomorulae*

Remarks and comparisons: The thick exine is very striking. By this phenomenon *V. reinhardtii* can be distinguished from *Verrucosisporites jenensis* Reinhardt & Schmitz in Reinhardt 1954b and *Verrucosisporites pseudomorulae* n. sp.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 392 m (Röt salinar).
Occurrence: Röt salinar of Hengelo; rare.

Verrucosisporites pseudomorulae n. sp.

Fig. 5c; Plate I, Figs. 4, 5.

Holotype: *Verrucosisporites pseudomorulae* n. sp. Single grain slide 31-HV-92; Plate I, Fig. 4.

Derivatio nominis: The new species reminds one of *Verrucosisporites morulae* Klaus 1960.

Diagnosis: Spores trilete, azonal, with approx. circular equator. Exine, 1.5–2 μ thick, distally covered by a dense irrigular ornamentation of polygonal verrucae (basis 1.5–3.5 μ, height 1.5–2 μ); proximally smaller (1.5–2 μ), regularly distributed verrucae are dominating; here a polygonal negative reticulum appears. Usually the verrucae are flattened, occasionally they are slightly gemmate. Equatorially 40–50 elements can be counted, diametrically 15–20. Distinct Y-mark with rays extending to 3/4–2/3 of the spore radius. Known size range 65–70 μ (holotype 68 μ).

Remarks and comparisons: A progressive transition between the irregularly distributed distal verrucae and the regularly placed proximal verrucae has been demonstrated. The species reminds one of *Verrucosisporites morulae* Klaus 1960 which, however, possesses rounded regularly placed verrucae. The same applies to *Verrucosisporites jenensis* Reinhardt and Schmitz in Reinhardt 1964 and *Verrucosisporites reinhardtii* n. sp.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 392 m (Röt salinar).

Occurrence: Röt salinar of Hengelo; rare.

Guttatisporites n. gen.

Type species: *Guttatisporites guttatus* n. sp., Plate II, Eigs. 1 A, B.

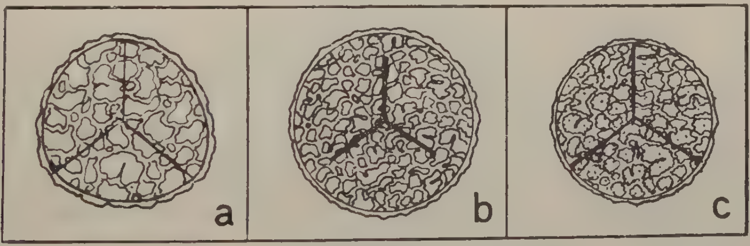


Fig. 6. *Guttatisporites*. a. *G. elegans*; b. *G. guttatus*; c. *G. microechinatus*

Diagnosis: Spores trilete, azonal, with approx. circular to convex-subtriangular equator. Exine densely covered by very irregularly shaped verruca-like elements. These elements show polygonal to crenulate outlines; they vary in size and shape. Bigger elements seem to have developed by the growing together of some small elements; they are mainly restricted to the distal spore surface. Between the elements a negative reticulum appears.

Remarks and comparisons: In spite of the bigger, complex elements *Guttatisporites* presents itself as a verrucate genus. It differs from *Verrucosisporites* Ibrahim 1933 emend. Smith *et al.* 1964 in that it possesses the characteristic exinal elements described.

Guttatisporites guttatus n. sp.

Fig. 6b; Plate 2, Figs. 1A, B.

Holotype: *Guttatisporites guttatus* n. sp. Single grain slide 31-HV-190; Plate II, Figs. 1A, B.

Diagnosis: Spores trilete, azonal, with circular equator. Diameter of holotype 95 μ. Exine, approx. 3.5 μ thick, densely covered by very irregularly shaped, low (approx. 1.5 μ) verruca-like elements; these show polygonal to slightly crenulate outlines; they vary in size and shape (basis 3–4 μ). Bigger elements, both proximally and distally existing, seem to have developed by the growing together of some smaller elements. The elements are unflattened, they possess a faint irregular relief. The narrow pits (approx. 0.5 μ) between the elements form a negative reticulum. Rather distinct Y-mark with trilete rays extending to 3/4–2/3 of the spore radius.

Remarks and comparisons: G. guttatus strikes by its truly circular equator; also specimens which are not proximo-distally flattened show a circular outline, this suggest a sphaerical shape of the spores. *Guttatisporites microechinatus* n. sp. differs by its small echinae superposed on the verrucae. *Guttatisporites elegans* n. sp. shows a subtriangular equator, longer trilete rays and bigger elements.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).

Occurrence: Röt salinar of Hengelo; rare.

Guttatisporites elegans n. sp.

Fig. 6a; Plate II, Figs. 4A, B.

Holotype: *Guttatisporites elegans* n. sp. Single grain slide 31-HV-228; Plate II, Figs. 4A, B.

Diagnosis: Spores trilete, azonal, with convex-subtriangular equator. Diameter of holotype 72 μ. Exine densely covered by very irregularly shaped verruca-like elements; these show polygonal to crenulate outlines; they vary in size and shape (basis 2–8 μ, height 1,5–2 μ); proximally only smaller elements can be found, distally the bigger elements predominate. The latter seem to have developed by the growing together of some small elements. The elements are unflattened, they possess a faint irregular relief. The trilete rays of the distinct Y-mark extend to the equator.

Remarks and comparisons: The shape of *G. elegans* seems related to an undescribed species illustrated by Couper and Hughes (1963, t. 1, f. 3) from the Dutch Lower Liassic; this species differs by the still more remarkably grown together elements. *Guttatisporites guttatus* n. sp. differs by its circular equator, by the shorter trilete rays and by the smaller average size of the verrucae. *Guttatisporites microechinatus* n. sp. possesses small echinae superposed on the verruca-like elements.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).

Occurrence: Only recognized in the shales between 405.50 and 406.80 m; very rare.

Guttatisporites microechinatus n. sp.

Fig. 6c; Plate II, Figs. 2, 3A, B.

Holotype: *Guttatisporites microechinatus* n. sp. Single grain slide 31-HV-275; Plate II, Fig. 2.

Diagnosis: Spores trilete, azonal, with approx. circular equator. Diameter of the holotype 89 μ. Exine, approx. 4.5 μ thick, densely covered by very irregularly shaped, low (approx. 1 μ) verruca-like elements; these show polygonal to strongly crenulate outlines; they differ strongly in size and shape. Bigger elements, existing both proximally and distally, seem to have developed by the growing together of some smaller elements. The elements are unflattened, they possess an irregular relief. Sometimes echina-like differentiations are superposed on the verrucae; usually one element bears one echina, but bigger elements may also possess two or more echinae. The narrow pits (approx. 0.5 μ) between the verrucae form a negative reticulum. The trilete rays extend to the equator.

Remarks and comparisons: The superposed echinae are only visible with high magnification. *G. microechinatus* differs from *Guttatisporites guttatus* n. sp. and *Guttatisporites elegans* n. sp. by its characteristic echina-bearing verrucae.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).
Occurrence: Röt salinar of Hengelo; rare.

SUBINFRATURMA *Tetradoapiculati* nov. subinfraturma

Diagnosis: Spores trilete, azonal, apiculate, still connected in tetrahedral tetrads.

Lapposisporites n. gen.

Type species: *Lapposisporites lapposus* n. sp., Plate III, Figs. 1A, B.

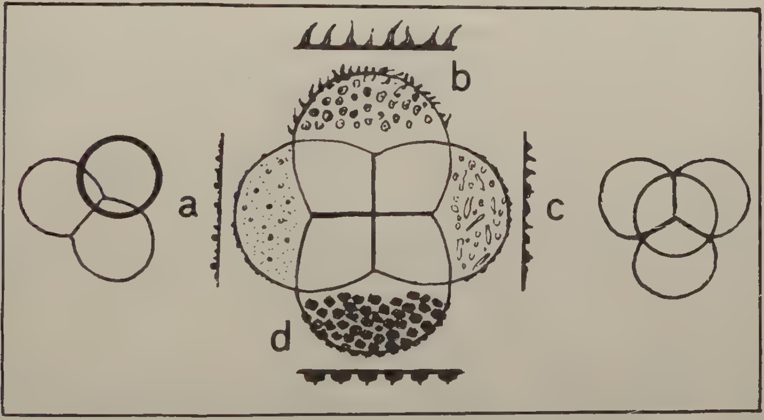


Fig. 7. *Lapposisporites*. a. *L. lapposus*; b. *L. villosus*; c. *L. armatus*; d. *L. loricatus*

Diagnosis: Spores trilete, azonal, apiculate, still connected in tetrahedral tetrads. Exine ornamentated with scabrae, grana, gemmae, verrucae, echinae, etc. in different combinations and/or ratios, depending on the species. Distal side semi-sphaerical, proximal side pyramidal; equator approx. circular.

Remarks and comparisons: Although the still connected spores do not show a tetrad mark the trilete character of *Lapposisporites* is indicated by the tetrahedral tetrads. The tetrads can be fossilized in three fundamental positions (Fig. 7). Superficially the genus reminds one of *Quadrisporites* Hennelly 1958 emend. Potonié & Lele 1961; this genus, however, differs by its tetragonal (square) or rhombic tetrads which suggest a monolete character. Moreover, investigations by Erdtman (1945) on the occurrence of tetrads of recent pollen show the exceptional appearance of both tetrahedral tetrads and tetragonal or rhombic tetrads within one plant species. *Ricciisporites* Lundblad 1954 emend. Lundblad 1959 differs by the presence of a distal sulcus and the absence of a pyramidal proximal side.

Lapposisporites lapposus n. sp.

Fig. 7a; Plate III, Figs. 1A, B, 2.

Holotype: *Lapposisporites lapposus* n. sp. Single grain slide 31-HV-108; Plate III, Figs. 1A, B.

Diagnosis: Spores trilete, azonal, apiculate, still connected in tetrahedral tetrads. Exine densely ornamentated by scabrae alternating with regularly placed grana and gemmae (max. height 1.5 μ). Biggest dimension of holotype 98 μ.

Comparisons: L. lapposus differs from *Lapposisporites villosus* n. sp., *Lapposisporites loricatus* n. sp. and *Lapposisporites armatus* n. sp. by its ornamentation of scabrae, grana and gemmae.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 392 m (Röt salinar).

Occurrence: Röt salinar of Hengelo; rare.

Lapposisporites villosus n. sp.

Fig. 7b; Plate V, Fig. 1.

Holotype: *Lapposisporites villosus* n. sp. Single grain slide 31-HV-98; Plate V, Fig. 1.

Diagnosis: Spores trilete, azonal, apiculate, still connected in tetrahedral tetrads. Exine densely ornamentated by long echinae (6–7 μ). Biggest dimension of holotype 120 μ.

Comparisons: L. villosus differs from *Lapposisporites lapposus* n. sp., *Lapposisporites loricatus* n. sp. and *Lapposisporites armatus* n. sp. by its striking echinate exine.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 392 m (Röt salinar).

Occurrence: Only recognized in the samples 34 (392 m) and 37 (405.50 m); very rare.

Lapposisporites armatus n. sp.

Fig. 7c; Plate IV, Fig. 1.

Holotype: *Lapposisporites armatus* n. sp. Single grain slide 31-HV-55; Plate IV, Fig. 1.

Diagnosis: Spores trilete, azonal, apiculate, still connected in tetrahedral tetrads. Exine ornamentated with spread echinae and verrucae with superposed echina-like differentiations (height 2–2.5 μ). Occasionally elements are grown together; in this case short narrow ridges can be formed. Biggest dimension of holotype 90 μ.

Remarks and comparisons: The verrucae with superposed echinae are very striking; there are progressive transitions between these elements and the normal echinae. This can be considered to be the principal difference with *Lapposisporites loricatus* n. sp. which is ornamentated by echina-bearing verrucae only. *Lapposisporites lapposus* n. sp. and *Lapposisporites villosus* n. sp. have a different exinal structure.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).
Occurrence: Only recognized in sample 37 (405.50 m); very rare.

Lapposisporites loricatus n. sp.

Fig. 7d; Plate IV, Fig. 2.

Holotype: *Lapposisporites loricatus* n. sp. Single grain slide 31-HV-151; Plate IV, Fig. 2.

Diagnosis: Spores trilete, azonal, apiculate, still connected in tetrahedral tetrads. Exine densely covered by approx. polygonal verrucae with superposed echina-like differentiations (basis elements 2.5–3 μ, distally 5 μ; height 3 μ). The pits between the elements form a negative reticulum. Biggest dimension of holotype 101 μ.

Remarks and comparisons: The dense ornamentation by verrucae with superposed echinae is very striking. No transitions to normal echinae can be seen as in *Lapposisporites armatus* n. sp. *Lapposisporites lapposus* n. sp. and *Lapposisporites villosus* n. sp. differ by their different exinal structure.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 392 m (Röt salinar).
Occurrence: Only recognized in the samples 34 (392 m) and 37 (405.50 m); very rare.

TURMA *Zonales* (Bennie & Kidston 1886) Potonié 1956
SUBTURMA *Zonotriletes* Waltz 1935
INFRATURMA *Cingulati* Potonié & Klaus 1954

Densoisporites Weyland & Krieger 1953

Type species: *Densoisporites velatus* Weyland & Krieger 1953, t. 4, f. 13, 14.

Densoisporites caretteae n. sp.

Fig. 8; Plate V, Fig. 2.

Holotype: *Densoisporites caretteae* n. sp. Single grain slide 31-HV-82; Plate V, Fig. 2.
Derivatio nominis: Mrs J. Levet-Carette, Laboratoire de Paléobotanique, Lille, France.

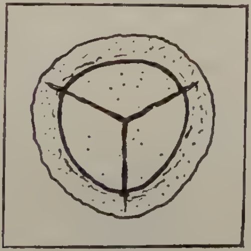


Fig. 8. *Densoisporites caretteae*

Diagnosis: Spores trilete, zonal. Equator of spore body and outline of cingulum subtriangular; diameter of holotype (cingulum included) 55 μ. Exine of spore body approx. 1 μ thick; finely infrastructured.

Cingulum scabrate with small circumequatorially situated folds; cingulum 5–7 μ wide. Trilete rays of the Y-mark extend into the cingulum; narrow labra.

Comparisons: D. caretteae reminds one of *Densoisporites perinatus* Couper 1958 (Jurassic – Lower Cretaceous); the latter species differs by its wider labra. Combined with a wider cingulum this also applies to *Densoisporites fissus* Reinhardt 1964, which also possesses, like *Densoisporites regularis* Danzé-Corsin & Laveine 1963, trilete rays extending to the outer margin of the cingulum.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 411.50 m (Röt salinar).
Occurrence: Röt salinar of Hengelo; very rare.

Pseudogravisporites n. gen.

Type species: *Pseudogravisporites reticulatus* n. sp., Plate V, Figs. 5A, B.
Derivatio nominis: The new genus reminds one of *Gravisporites* Bharadwaj 1954.

Diagnosis: Spores trilete, zonal. Equator of spore body and outline of cingulum approx. circular to subtriangular. Exine laevigate to scabrate. Very narrow trilete sutures situated between strongly developed labra which form rather wide ridges with crenulate margins; they terminate abruptly just before the equator of the spore body.

Remarks and comparisons: The genus reminds one of *Gravisporites* (al. *Cadiospora*) *sphaerus* (Butterworth & Williams 1954) Bharadwaj 1954, the type species of *Gravisporites* Bharadwaj 1954. This species, however, is characterized by a thickening of the equator of the spore (crassitudo). *Pseudogravisporites* does not show this equatorial thickening: the cingulum is lighter coloured than the exine of the spore body. Also *Cadiospora* Kosanke 1950 emend. Venkatachala & Bharadwaj 1964 is characterized by a thickened equatorial exine. *Lycospora* Schopf, Williams & Bentall 1944 emend. Potonié & Kremp 1954 includes smaller species with longer and narrower labra. *Polimorphisporites* Alpern 1958, at least the type species *Polymorphisporites laevigatus* Alpern 1958 differs by its trilete rays of unequal length and its less pronounced labra.

Pseudogravisporites reticulatus n. sp.

Fig. 9; Plate V, Figs. 5 A, B.

Holotype: *Pseudogravispoirtes reticulatus* n. sp. Single grain slide 31-HV-160; Plate V, Figs. 5A, B.

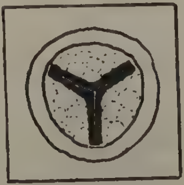


Fig. 9. *Pseudogravisporites reticulatus*

Diagnosis: Spores trilete, zonal; equator of spore body and outline of cingulum subtriangular; diameter (cingulum included) 58–62 μ

(holotype 61 μ). Exine laevigate to scabrate; distally low muri make a very vague reticulate structure. Very narrow trilete sutures situated between wide ridge-like labra (approx. 5 μ wide); the margins of the labra are slightly crenulate; they terminate abruptly just before the equator of the spore body.

Remark: The vague reticulate structure is only visible with phase-contrast microscopes.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).
Occurrence: Only recognized in the shales between 405.50 and 406.80 m; rare.

Anguisporites Potonié & Klaus 1954

Type species: *Anguisporites anguinus* Potonié & Klaus 1954, t. 10, f. 4.

Anguisporites tenuis n. sp.

Fig. 10; Plate V, Fig. 3.

Holotype: *Anguisporites tenuis* n. sp. Single grain slide 31-HV-09; Plate V, Fig. 3

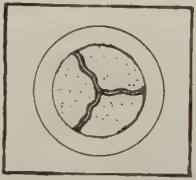


Fig. 10. *Anguisporites tenuis*

Diagnosis: Spores trilete, zonal; equator of spore body and outline of cingulum approx. circular; relatively small diameter (30–35 μ; holotype 32 μ). Exine probably finely scabrate. Trilete rays extend to the equator of the spore body; the sutures are situated between more or less wavy ridge-like labra.

Remarks and comparisons: The characteristics of *A. tenuis* are badly pronounced; the wavy trilete rays do not appear as clear dark differentiations like the Y-mark of the Permian *Anguisporites anguinus* Potonié & Klaus 1954, *Anguisporites intonsus* Wilson 1962 and *Anguisporites contortus* Wilson 1962; moreover these species are bigger. Cf. *Anguisporites anguinus* Grebe 1957 seems more related to *A. tenuis*.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).
Occurrence: Röt salinar of Hengelo; rare.

Paralundbladispora n. gen.

Type species: *Paralundbladispora quadriiuga* n. sp., Plate IV, Fig. 4.
Derivatio nominis: The new genus seems related to *Lundbladispora* Balme 1963.

Diagnosis: Spores trilete, zonal, usually still connected in tetrahedral tetrads. Equator of spore body approx. circular to subtriangular. Exine finely structured or infrastructured. Narrow cingulum, situated proximal of the equator. Proximal side with subpyramidal shape. The rare single specimens show a tetrad mark with thickened labra.

Remarks and comparisons: We consider the occurrence in still connected tetrahedral tetrads a generic characteristic; single spores are very rare. Superficially the tetrads remind one of tetrads of *Circulina*

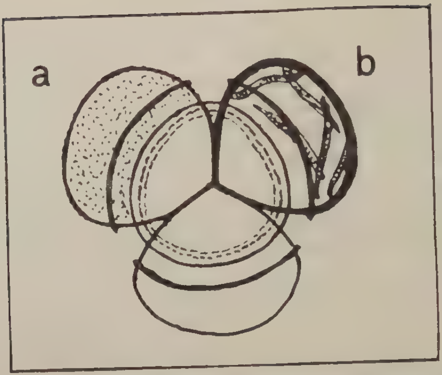


Fig. 11.
Paralundbladispora.
a. *P. quadriiuga*;
b. *P. vieta*

(Malavkina 1949) ex Klaus 1960 which is characterized, however, by a circumequatorial thinning of the exine. The cingulum of Paralundbladispora is clearly projecting. Moreover, the proximal side of *Circulina* is more rounded, it shows a very small Y-mark. *Lundbladispora* Balme 1963, sometimes also occurring in tetrads, seems very related but differs by the truly equatorial cingulum and the eccentrically placed papillate intexine.

Paralundbladispora quadriiuga n. sp.

Fig. 11a; Plate IV, Figs. 4, 5.

Holotype: *Paralundbladispora quadriiuga* n. sp. Single grain slide 31-HV-268; Plate IV, Fig. 4.

Diagnosis: Spores trilete, zonal, usually still connected in tetrahedral tetrads. Equator of spore body approx. circular to subtriangular. Exine scabrate to finely granulate; exine approx. 1 μ thick. Narrow cingulum, situated proximal of the equator. Proximal side subpyramidal. Single specimens show the tetrad mark with the thickened irregularly wavy labra which approximately extend to the equator (Plate IV, Fig. 5). Biggest dimension of the holotype 57 μ.

Remarks and comparisons: Because of the proximal position of the cingulum polar flattened specimens, both single spores and spores forming part of a tetrad do not show the narrow cingulum clearly. It appears as proximal folds parallel to the equator. Equatorially flattened specimens of the tetrads, however, demonstrate the cingulum very clearly. *P. quadriiuga* reminds one of *Lundbladispora nejburgii* Schulz 1964 which may be compared with the microspores of *Pleuromeia rossica* Nejburg 1960; it differs by occurring in tetrads and by slightly narrower labra. *Paralundlbadispora vieta* n. sp. differs by a thick infrastructured exine.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).

Occurrence: Röt salinar of Hengelo; rare. In the upper part of the overlying Röt pelites (transition to Muschelkalk) the species is more frequent.

Paralundbladispora vieta n. sp.

Fig. 11b; Plate IV, Figs. 3A, B.

Holotype: *Paralundbladispora vieta* n. sp. Single grain slide 31-HV-230; Plate IV, Figs. 3A, B.

Diagnosis: Spores trilete, zonal, only recognized in still connecting tetrahedral tetrads. Equator of spore body approx. circular to subtriangular. Exine 2.5 3 μ thick, smooth with fine infrastructure. Narrow cingulum, situated proximal of the equator. Proximal side of a single spore subpyramidal. The spores are strongly folded. Biggest dimension of holotype 66 μ.

Remarks and comparisons: As for the visibility of the proximal cingulum, compare *Paralundbladispora quadriiuga* (remarks, p. 338). The latter species differs from *P. vieta* by its thinner scabrate-granulate exine.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).

Occurrence: Röt salinar of Hengelo; very rare. In the upper part of the overlying Röt pelites (transition to Muschekallk) the species is more frequent.

INFRATURMA *Zonati* Potonié & Kremp 1954

Kraeuselisporites Leschik 1956a emend. Jansonius 1962

Type species: *Kraeuselisporites dentatus* Leschik 1956a, t. 4, f. 21.

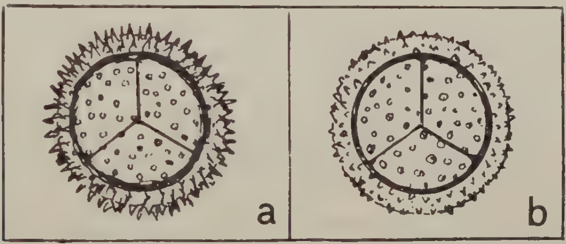


Fig. 12. *Kraeuselisporites*. a. *K. hystrix*; b. *K. hoofddijkensis*

Remarks and comparisons: We want to restrict *Kraeuselisporites* to forms with a distal echinate spore-exine and an echinate zona. *Styxisporites* Cookson and Dettmann 1958 differs by possessing a laevigate zona.

Kraeuselisporites hystrix n. sp.

Fig. 12a; Plate VI, Fig. 1.

Holotype: *Kraeuselisporites hystrix* n. sp. Single grain slide 31-HV-301; Plate VI, Fig. 1.

Diagnosis: Spores trilete, zonal; equator of spore body and outline of zona approx. circular to subtriangular. Diameter (zona included) 70–80 μ (holotype 75 μ). Exine of spore body 1.5–3 μ thick, proximally smooth, distally ornamentated by long echinae (basis 2–3 μ, length 6–7 μ). Zona 3–5 μ wide, also covered by long echinae. Trilete rays extend to the equator of the spore body; they are accompanied by narrow, slightly thickened labra.

Remarks and comparisons: The long echinae may break easily during fossilisation. *K. hystrix* differs from *Kraeuselisporites hoofddijkensis* n. sp. by its longer echinae.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).

Occurrence: Röt salinar of Hengelo; rare.

Kraeuselisporites hoofddijkensis n. sp.

Fig. 12b; Plate VI, Figs. 3, 4.

Holotype: *Kraeuselisporites hoofddijkensis* n. sp. Single grain slide 31-HV-302; Plate VI, Fig. 4.

Derivatio nominis: Fort Hoofddijk, Utrecht, the Netherlands; former fort, at present Palaeobotanical and Pollenmorphologicol laboratories.

Diagnosis: Spores trilete, zonal; equator of spore body and outline of zona approx. circular to subtriangular. Diameter (zona included) 55–70 μ (holotype 59 μ). Exine of spore body 2–4 μ thick, proximally smooth with fine infrastructure, distally ornamentated by echinae. The echinae show a diverging variability in shape; elements with a wide basis (max. 4 μ) show a polygonal outline, smaller elements (from 1 μ) are more or less circular; length of echinae 2–3.5 μ. Zona 2–2.5 μ wide, also covered by echinae. Trilete rays extend to the equator of the spore body; they are accompanied by narrow slightly thickened labra which are fan-shaped at the ends.

Remarks and comparisons: The species shows an important variation in size and shape of the echinae; however, there is always progressive transition, so a specific separation does not seem desirable. *K. hoofddijkensis* differs from *Kraeuselisporites hystrix* n. sp. by its shorter echinae. Frequently there are tendencies to a release of the zona.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).

Occurrence: Most frequent zonal spore in the Hengelo Röt salinar; never high percentages. Also recognized in the overlying Röt pelites.

TURMA *Monoletes* Ibrahim 1933

Saturnisporites Klaus 1960

Type species: *Saturnisporites fimbriatus* Klaus 1960, t. 32, f. 32, 33.

Remarks and comparisons: Klaus (1960) dealt with the relation *Aratrisporites* Leschik 1956a – *Saturnisporites* Klaus 1960; he separates the genera strictly. Recently this subject was discussed again by BHARADWAJ and SINGH (1964); they do not find any important differences. Because of differences existing in equatorial flattened specimens, however, we want to follow Klaus. In equatorial view *Aratrisporites* shows a slightly concave proximal outline (KLAUS 1960, t. 44, f. 41); *Saturnisporites* differs by a straight to slightly convex outline (Plate XIII, fig. 4). These differences suggest a different shape of the spores and justify a separation. We are not convinced of the zonal character of the genus.

Up till now both *Saturnisporites* and *Aratrisporites* have only been found in Upper Triassic assemblages; our findings indicate a still earlier appearance of these interesting monolete spores.

Saturnisporites praevius n. sp.

Fig. 13; Plate XIII, Figs. 3, 4.

Holotype: *Saturnisporites praevius* n. sp. Single grain slide 31-HV-126; Plate XIII, Fig. 3.

Diagnosis: Spores monolete, zonal (?), with elliptical equator. Proximal exine with fine infrastructure; the distal exine seems strongly

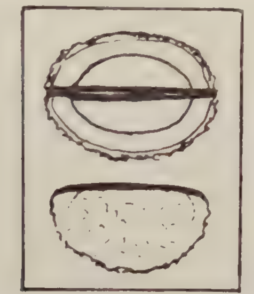


Fig. 13. *Saturnisporites praevius*

fibrous, it can easily be deformed, causing an irregular outline with projecting "fibres". Very narrow monolete suture accompanied by pronounced dark labra which extend into the "zona". "Zona" 6–9 μ wide. In equatorial view the proximal outline appears straight to slightly convex. Known size range 54–62 μ (holotype 59 μ).

Remarks and comparisons: Specimens of *S. praevius* are always badly preserved; we are not convinced of the zonal character. *Saturnisporites fimbriatus* Klaus 1960, *Saturnisporites palettae* Klaus 1960 and *Saturnisporites fischeri* Klaus 1960 differ by possessing regularly shaped hairs which cannot be confused with the fibre-like projections of *S. praevius*.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 392 m (Röt salinar).

Occurrence: Röt salinar of Hengelo; rare. Also recognized in the upper part of the Röt pelites (transition to Muschelkalk); more frequent.

ANTETURMA *Pollenites* Potonié 1931
TURMA *Saccites* Erdtman 1947
SUBTURMA *Monosaccites* (Chitaley 1951) Potonié & Kremp 1954
INFRATURMA *Triletesacciti* Leschik 1956a

Nuskoisporites Potonié & Klaus 1954 emend. Klaus 1963a

Type species: *Nuskoisporites dulhuntyi* Potonié and Klaus 1954, t. 10, f. 5.

Nuskoisporites inopinatus n. sp.

Fig. 14; Plate VII, Figs. 1A, B.

Holotype: *Nuskoisporites inopinatus* n. sp. Single grain slide 31-HV-179; Plate VII, Figs. 1A, B.

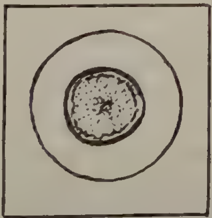


Fig. 14. *Nuskoisporites inopinatus*

Diagnosis: Pollen radial, monosaccate, trilete. Equator of central body approx. circular to subtriangular. Proximal exoexine infragranulate; small short-rayed trilete Y-mark in proximal intexine, only visible with high magnification. Saccus imperfectly and finely infrareticulate. Because of the thin exine a distinct saccus-margin ("limbus") is absent. Narrow distal saccus-overlap with irregularly shaped contact edge. Diameter of holotype 85 μ.

Remarks and comparisons: The Y-mark does not appear in the proximal exoexine. Usually the recognized specimens of *N. inopinatus* are badly preserved. However, the holotype shows sufficient details to compare it with the Permian representatives of *Nuskoisporites*. In some aspects *N. inopinatus* reminds one of the American *Nuskoisporites crenulatus* Wilson 1962 which, however, possesses a deeply crenulate contact edge. *Nuskoisporites triangularis* (Metha 1944) Potonié & Lele 1961 (≡ *Nuskoisporites gondwanensis* Balme & Hennelly 1956) and *Nuskoisporites rotatus* Balme & Hennelly 1956 from the Gondwana region do not show distinct saccus-margins, but differ by the presence of a clearly visible Y-mark. The European species *Nuskoisporites dulhuntyi* Potonié & Klaus 1954 and *Nuskoisporites klausii* Grebe 1947 are characterized both by a distinct margin and a distinct Y-mark.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).

Occurrence: Only recognized in the shales between 405.50 and 406.80 m; rare.

SUBTURMA *Disaccites* Cookson 1947

INFRATURMA *Disacciatriletes* (Leschik 1956a) Potonié 1958

Voltziaceaesporites Klaus 1964

Type species: *Voltziaceaesporites heteromorpha* Klaus 1964, t. 2, f. 19.

Voltziaceaesporites heteromorpha Klaus 1964

Fig. 15; Plate VIII, Figs. 3, 4, 5.

Holotype: *Voltziaceaesporites heteromorpha* Klaus 1964, t. 2, f. 19.

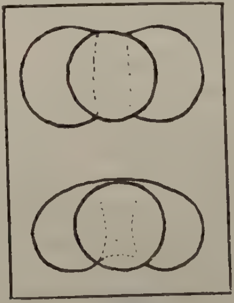


Fig. 15. *Voltziaceaesporites heteromorpha*

Remarks: Our forms correspond to the specific description by KLAUS (1964). Within the variation of *V. heteromorpha* monosaccate, trisaccate and platysaccoid forms are rather common. There are also divergences in the thickness of the proximal exine of the central body. Observed size range 70–135 μ.

Occurrence: V. heteromorpha is the most common species in the Hengelo Röt salinar; less frequent in the Röt pelites. Also known from French, German and Alpine Upper Bunter or equivalents (KLAUS 1964). In Muschelkalk and Keuper assemblages the species may still be present in decreased percentages.

Alisporites Daugherty 1941

Type species: *Alisporites opii* Daugherty 1941, t. 34, f. 2.

Alisporites microreticulatus Reinhardt 1964a

Fig. 16a; Plate XIII, Figs. 1, 2A, B.

Holotype: *Alisporites microreticulatus* Reinhardt 1964a, t. 2, f. 5, 6.

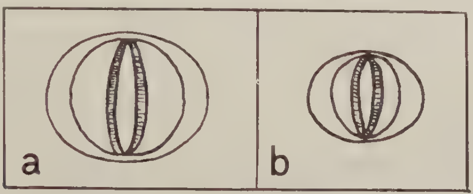


Fig. 16. *Alisporites*. a. *A. microreticulatus*; b. *A. grauvogeli*

Remarks and comparisons: Our forms correspond to the specific description by Reinhardt (1964a). The very finely infrareticulate sacci are exceedingly striking; they are radially structured. Compared with the other bisaccate species from the assemblage described *A. microreticulatus* is remarkably dark-brown coloured. The fundamentally fusiform germinal area may show diverging shapes, due to fossilisation. In a few cases specimens with a clear reduced trilete mark in the proximal exoexine were recognized (Plate XIII, Figs. 2A, B), there are no other differences with the dominant alete forms. This feature may suggest a trilete tendency within the variation of *A. microreticulatus*. Observed size range 68–128 μ.

The species differs from *Alisporites grauvogeli* Klaus 1964 by its characteristic infrareticulum and by a bigger average size.

Occurrence: Regularly recognized in the Hengelo Röt salinar; never in high percentages. Reinhardt (1964a) reports the species from the Lower Röt of Thüringen (Germany).

Alisporites grauvogeli Klaus 1964

Fig. 16b; Plate XIV, Figs. 5, 6.

Holotype: *Alisporites grauvogeli* Klaus 1964, t. 4, f. 38.

Remarks and comparisons: Our forms correspond to the specific description by Klaus (1964); we observed a wider size range (40–80 μ, Klaus: 60–80 μ). The fundamentally fusiform germinal area may show diverging shapes due to fossilisation. Compared with *Alisporites microreticulatus* Reinhardt 1964a, *A. grauvogeli* possesses a considerably coarser infrareticulum.

Occurrence: Regularly recognized both in the Röt salinar and in the Röt pelites of Hengelo. Klaus (1964) mentions *A. grauvogeli* from German, French and Alpine Upper Bunter or equivalents.

Colpectopollis Pflug 1953 emend.

Type species: *Colpectopollis occupatus* Pflug 1953, t. 17, f. 7, 8, 9.

Diagnosis: Pollen bisaccate, alete. Elliptical outline both in polar view and in equatorial view; this is due to the original ellipsoid shape of the pollen grains. Central body with thickened proximal exoexine.

Sacci haploxylonoid, equatorially interconnected. Very indistinct distal germinal area which is fundamentally fusiform. Both the thickened proximal exine of the central body and the unthickened distal exine can be longitudinally folded. This happens very frequently in a very characteristic way (see remarks).

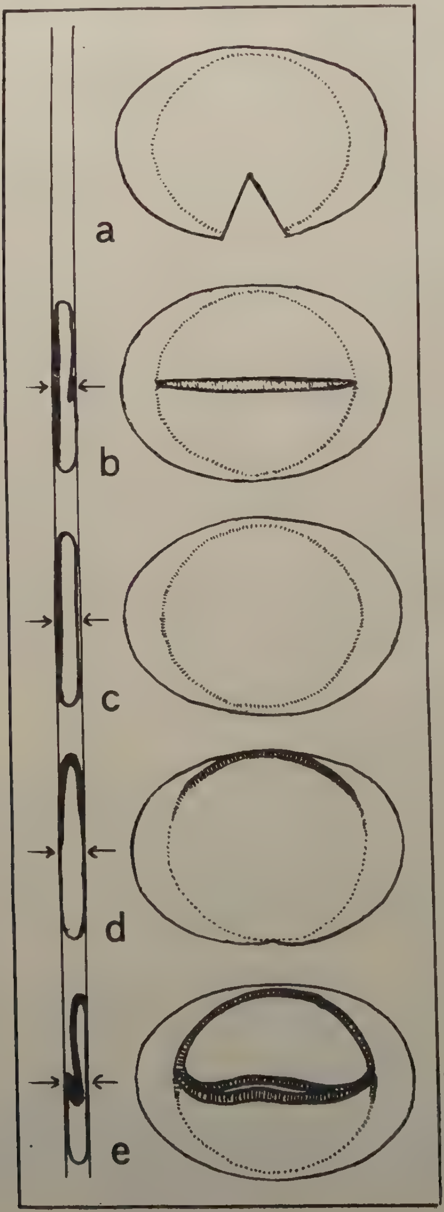


Fig. 17.
Colpectopollis ellipsoideus.
- a. torn specimen
- b. distal folding
- c. polar view
- d. equatorial view
- e. proximal folding

Remarks and comparisons: Pflug (1953) described his genus *Colpectopollis* as follows: "Mit Resten von Luftsäcken. Germinalapparat besteht nur aus der Kammgerminal. Porus rückgebildet". Within the assemblage described we found specimens which are well comparable with Pflug's illustrations of *Colpectopollis* and of his "Siegelsum M-Typus". However the author considers the "Kammgerminal" nothing but a longitudinal fold in the thickened proximal exine. Differences in the projection of the infrabaculate proximal exine cause a seeming ridge, split by a seeming crack (Fig. 17e). Also the unthickened distal exine is sensitive to folding (Fig. 17b). Specimens in polar view without any folding are very rare (Fig. 17c). Specimens in equatorial view show clearly the thickened proximal exine and the elliptical outline (Fig. 17d). Because of the original ellipsoid shape the pollen grains do not show any preference for their position during sedimentation; consequently they can be fossilized in diverging positions.

On account of our reconstructions (Fig. 17) we have to disagree with Pflug's concept of a germinal function of the longitudinal ridges; we also deny the existence of a "rückgebildete Porus".

Although the presence of the characteristic folds is due to fossilisation the genus *Colpectopollis* can be maintained; the folds, combined with the ellipsoid shape are useful generic characteristics.

It seems likely that *Unatextisporites* Leschik 1956a also possesses a seeming crack (compare Leschik 1956a, t. 8, f. 7 with Pflug 1953, t. 17, f. 15, 16 and our Plate IX, Fig. 3).

Also torn specimens (Fig. 17a) are frequent; they can be compared with *Schismatosporites* Nilsson 1958. The polar view, without folds, reminds one of *Sulcatisporites* Leschik 1956a emend. Bharadwaj 1962 which, however, possesses distally inclined sacci. The general shape of *Ovalipollis* Krutzsch 1955 emend. Klaus 1960 may be related, but according to Klaus (1960) this genus possesses a true exinal crack. *Chordasporites* Klaus 1960 differs by its saccus interconnecting exoexinal strand and the absence of an ellipsoid shape.

Colpectopollis ellipsoideus n. sp.

Fig. 17; Plate IX, Figs. 1, 2, 3, 4, 5.

Holotype: *Colpectopollis ellipsoideus* n. sp. Single grain slide 31-HV-218; Plate IX, Fig. 3.

Diagnosis: Pollen bisaccate, alete. Elliptical outline both in polar view and in equatorial view; this is due to the original ellipsoid shape of the pollen grain. Equator of the central body approx. circular to longitudinally elliptical. Central body with proximally thickened exine (3–3.5 μ). Sacci haploxylonid, equatorially interconnected. Very indistinct distal germinal area which is fundamentally fusiform. Both the thickened proximal exine of the central body and the unthickened distal exine can be longitudinally folded. This happens very frequently and in a very characteristic way (compare emended generic description, remarks.) Known size range 70–100 μ (holotype 77 μ).

Remarks and comparisons: Reconstructing the original shape of the pollen grain it has been demonstrated that the equatorial exine is not thickened (Fig. 17d); so in polar view the outline of the central body shows very indistinctly. This in contrast with *Colpectopollis occupatus* Pflug 1953.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).

Occurrence: Röt salinar of Hengelo; regularly recognized but never in high percentages. Also present in the upper part of the overlying Röt pelites; more frequent.

Chordasporites Klaus 1960

Type species: *Chordasporites singulichorda* Klaus 1960, t. 33, f. 45.

Remarks: Bisaccate pollen grains showing the striking exinal strand interconnecting the sacci may be considered monstrousities. In all probability the phenomenon of a chorda appears within several form-genera. Because of the important stratigraphical value of *Chordasporites* (Klaus 1960, 1964), however, accidental deformations are out of the question. The occurrence of the genus is mainly restricted to Triassic assemblages (Klaus 1960, 1964; De Jersey 1962) but also in Upper Permian rare representatives of *Chordasporites* are to be expected (Klaus 1963b).

Chordasporites voltziaformis n. sp.

Fig. 18; Plate VII, Figs. 4A, B.

Holotype: *Chordasporites voltziaformis* n. sp. Single grain slide 31-HV-19; Plate VII, Figs. 4A, B.

Derivatio nominis: The new species may be derived from *Voltziaceaesporires heteromorpha* Klaus 1964.

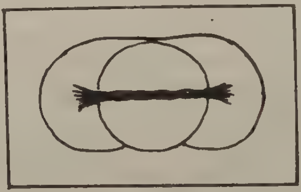


Fig. 18. *Chordasporites voltziaformis*

Diagnosis: Pollen bisaccate, alete; shaped essentially like *Voltziaceaesporites heteromorpha* Klaus 1964 but provided with a longitudinal saccus-interconnecting chorda. Chorda approx. 4 μ wide, fan-wise shading off into the saccus infrareticulum, which is radially structured. Known size range 70–80 μ (holotype 79 μ).

Remarks and comparisons: Specimens of *C. voltziaformis* are usually badly preserved. Apart from the chorda there are great similarities to *Voltziaceaesporites heteromorpha*, from which our species may be derived. *Chordasporites magnus* Klaus 1964 seems highly related, but differs by its bigger size. *Chordasporites singulichorda* Klaus 1960 and *Chordasporites australiensis* De Jersey 1962 do not show any relation to *V. heteromorpha*.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 404 m (Röt salinar).

Occurrence: Röt Group of Hengelo; rare.

Falcisporites Leschik 1956b emend. Klaus 1963a

Type species: *Falcisporites* (al. *Pityosporites*) *zapfei* (Potonié & Klaus 1954) Leschik 1956b; Potonié and Klaus 1954, t. 10, f. 9.

Falcisporites snopkovae n. sp.

Fig. 19; Plate VII, Figs. 3A, B.

Holotype: *Falcisporites snopkovae* n. sp. Single grain slide 31-HV-194; Plate VII, Figs. 3A, B.

Derivatio nominis: Mrs P. Snopková, Geologický ústav D. Štúra, Bratislava, Czecho-Slovakia.

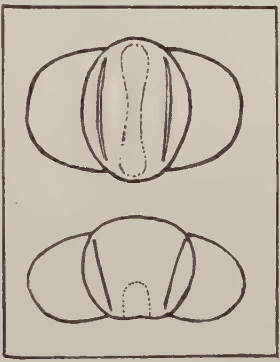


Fig. 19. *Falcisporites snopkovae*

Diagnosis: Pollen bisaccate, alete. Equator of central body usually transversely elliptical but occasionally tendencies to circular and even longitudinally elliptical outlines. Proximal exoexine finely infrareticulate to finely granulate at the proximal pole. Sacci haploxylonoid, hardly or not distally inclined, laterally not interconnected; meshes of the regularly shaped infrareticulum 2–3 μ wide. Distal germinal area more or less distinctly limited, lemniscatoid shape, usually accompanied by narrow transversal folds. Known size range 80–92 μ (holotype 84 μ).

Remarks and comparisons: Compared with most of the other bisaccate species in the assemblage described, the sacci of *F. snopkovae* are rather coarsely infrareticulate. *Falcisporites zapfei* (Potonié & Klaus 1954) Leschik 1956b is very related, but this Upper Permian species differs by a still coarser infrareticulum which is irregularly and imperfectly shaped. Specimens with a transversely elliptical equator do not exist within the variation of *F. zapfei*.

Freudenthal (1964) illustrates three specimens of "*F. zapfei*"; one of them, however, must be considered to be *F. snopkovae* (t. 2, f. 2); the other two specimens belong to *Paravesicaspora planderovae* n. sp. (t. 2, f. 1, 3).

F. snopkovae differs from *Triadispora falcata* Klaus 1964 by the absence of a tetrad mark and by its relatively coarse infrareticulum.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).
Occurrence: Röt salinar of Hengelo; rare.

Paravesicaspora Klaus 1963a

Type species: *Paravesicaspora* (al. *Sulcatisporites*) *splendens* (Leschik 1956b) Klaus 1963a; Leschik 1956b, t. 22, f. 10.

Paravesicaspora planderovae n. sp.

Fig. 20; Plate VIII, Figs. 1A, B, 2.

Holotype: *Paravesicaspora planderovae* n. sp. Single grain slide 31-HV-54; Plate VIII, Figs. 1A, B.

Derivatio nominis: Mrs E. Planderová, Geologický ústav D. Štúra, Bratislava, Czecho-Slovakia.

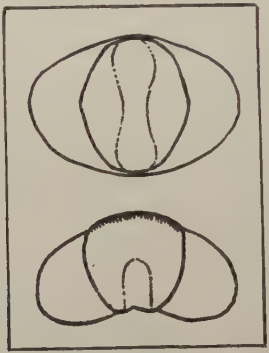


Fig. 20. *Paravesicaspora planderovae*

Diagnosis: Pollen bisaccate, alete. Equator of central body transversely elliptical to subangular (rhombic). Proximal exoexine finely infrareticulate to infragranulate. Sacci haploxylonoid, distally inclined, finely infrareticulate. In polar view a narrow lateral saccus-interconnection is visible. Smooth distal germinal area, more or less distinctly limited, usually clearly lemniscatoid. Known size range 70–94 μ (holotype 90 μ).

Remarks and comparisons: Because of fossilisation sometimes the lateral exoexinal saccus-interconnections are ruptured; in this case specimens with a more or less *Falcisporites*-like habitus can be formed (Freudenthal 1964, t. 2, f. 3: "*Falcisporites zapfei*"). These forms differ from *Falcisporites zapfei* (Potnié & Klaus 1954) Leschik 1956b and *Falcisporites snopkovae* n. sp. by a much finer saccus infrareticulum. *P. planderovae* also differs from *Paravesicaspora splendens* (Leschik 1956b) Klaus 1963a by a finer infrastructure of the bladders.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).

Occurrence: Röt salinar of Hengelo; rare.

Microcachryidites (Cookson 1947) ex Couper 1953

Type species: *Microcachryidites antarcticus* Cookson 1947, t. 14, f. 19.

Microcachryidites doubingeri Klaus 1964

Fig. 21; Plate VII, Figs. 2A, B.

Holotype: *Microcachryidites doubingeri* Klaus 1964, t. 3, f. 27.

Remarks: Our specimens correspond to the specific description by Klaus (1964). The thick exine is very striking.

Occurrence: Klaus (1964) reported *M. doubingeri* from French and Italian Muschelkalk assemblages. We recognized the species in very low percentages in the Hengelo

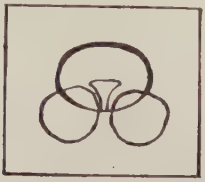


Fig. 21. *Microcachryidites doubingeri*

Röt salinar; the percentages increase, however, in the upper part of the Röt pelites (transition to Muschelkalk).

INFRATURMA *Disaccitriletes* Leschik 1956a.

Triadispora Klaus 1964

Type species: *Triadispora plicata* Klaus 1964, t. 2, f. 15.

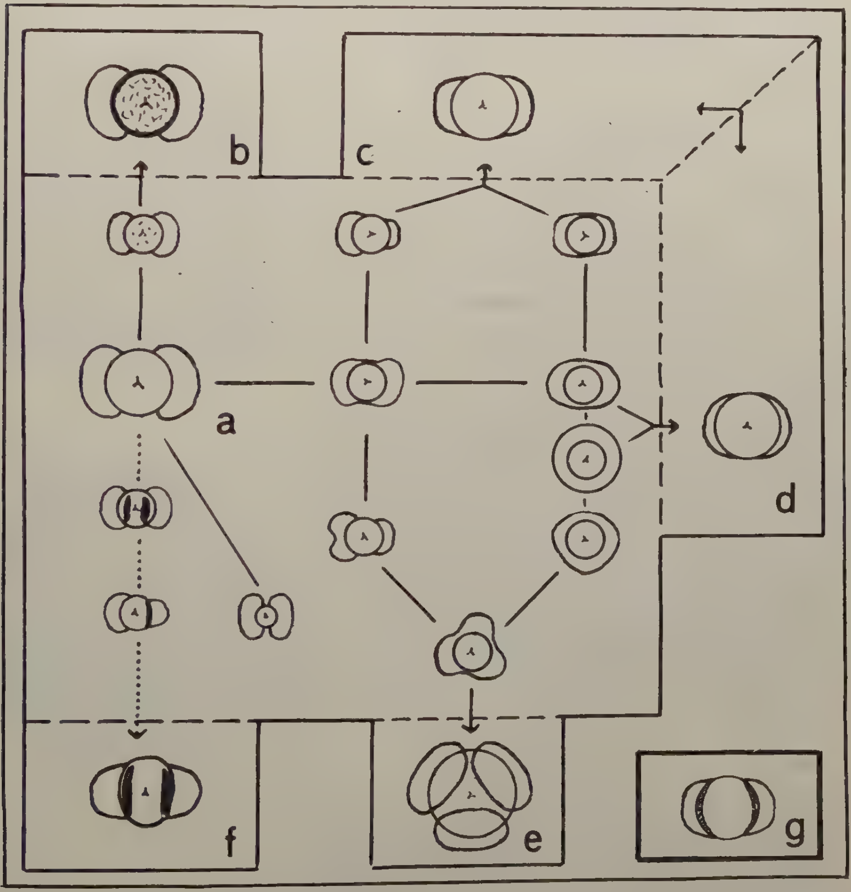


Fig. 22. The variation of *Triadispora*. a. *T. crassa* with its transitions to the other species; b. *T. plicata*; c. *T. staplini*; d. *T. epigona*; e. *T. muelleri*; f. *T. falcata*; g. *Klausipollenites staplini*

Remarks and comparisons: In 1958 KLAUS already reported the existence of bisaccate trilete pollen which should be characteristic for European Lower Triassic assemblages. In 1964 he described the genus *Triadispora*. Apart from abnormal forms ("Forma Y") KLAUS (1964) distinguished five different species: *T. staplini* (we do not consider *T. staplini* identical with *Klausipollenites staplini* Jansonius 1962), *T. crassa*, *T. falcata*, *T. epigona* and *T. plicata*. Moreover, a sixth species can be distinguished: *T. muelleri* (≡ *Nuskoisporites muelleri* Reinhardt and Schmitz in REINHARDT 1964b).

In the assemblage described, more than 80 % of the *Triadispora*-forms belong to *Triadispora crassa*. The variation of this species turns out to be very diverging and includes amongst others progressive transitions to the other *Triadispora*-species (Fig. 22). This may be an argument for placing these species within the variation of *T. crassa*, in order to avoid a subjective specific subdivision. For stratigraphical reasons, however, a separation remains desirable (compare p. 326). The variation of the genus *Triadispora* reminds one of the analogue divergences in the pollen in situ of *Ullmannia frumentaria*, investigated by GREBE and SCHWEITZER (1962). A wide variation combined with the occurrence of abnormal forms is also demonstrated within the striate pollen studied by BHARADWAJ (1962). Frequently a wide variation of recent coniferal saccate pollen is due to interspecific hybridizing. For example the hybrid *Pinus uncinata* × *Pinus silvestris* produces pollen grains possessing both abnormal shapes and varying dimensions compared with the parents (AYTUG 1962).

In the symposium "Evolution" (Amsterdam 1959) Sirks mentioned the widespread opinion according to which interspecific hybridizing might be an important factor in plant evolution. The creation of botanical interspecific hybrids may lead to an explosion of new phenotypes (SIRKS 1960).

An evolutionary trend within the genus *Triadispora* might explain the differences in relative quantitative distribution of its species in other localities (compare p. 325). However, to prove this preliminary impression we need more data about the horizontal and vertical occurrence of this interesting genus.

FREUDENTHAL's (1964) illustrations of his genus *Eridospollenites* are concerned with *Triadispora*. *Limitisporites* Leschik 1956b emend. Potonié 1958 differs from *Triadispora* by the presence of a structureless exoexinal area around the Y-mark (for the taxonomical problem with regard to *Limitisporites*, *Jugasporites*, *Illinites* and *Eridospollenites* we refer to the description of *Illinites*, p. 353).

Triadispora crassa Klaus 1964

Fig. 22a; Plate X, Figs. 1–6; Plate XI, Figs. 1–12; Plate XII, Fig. 7.

Holotype: *Triadispora crassa* Klaus 1964, t. 1, f. 2.

Remarks and comparisons: In spite of distinguishing five more species of *Triadispora* the variation of *T. crassa* still remains very diverging (Fig. 22a). This is mainly due to the multitude in transitional forms between this species and *T. staplini*, *T. plicata*, *T. epigona*, *T. falcata*

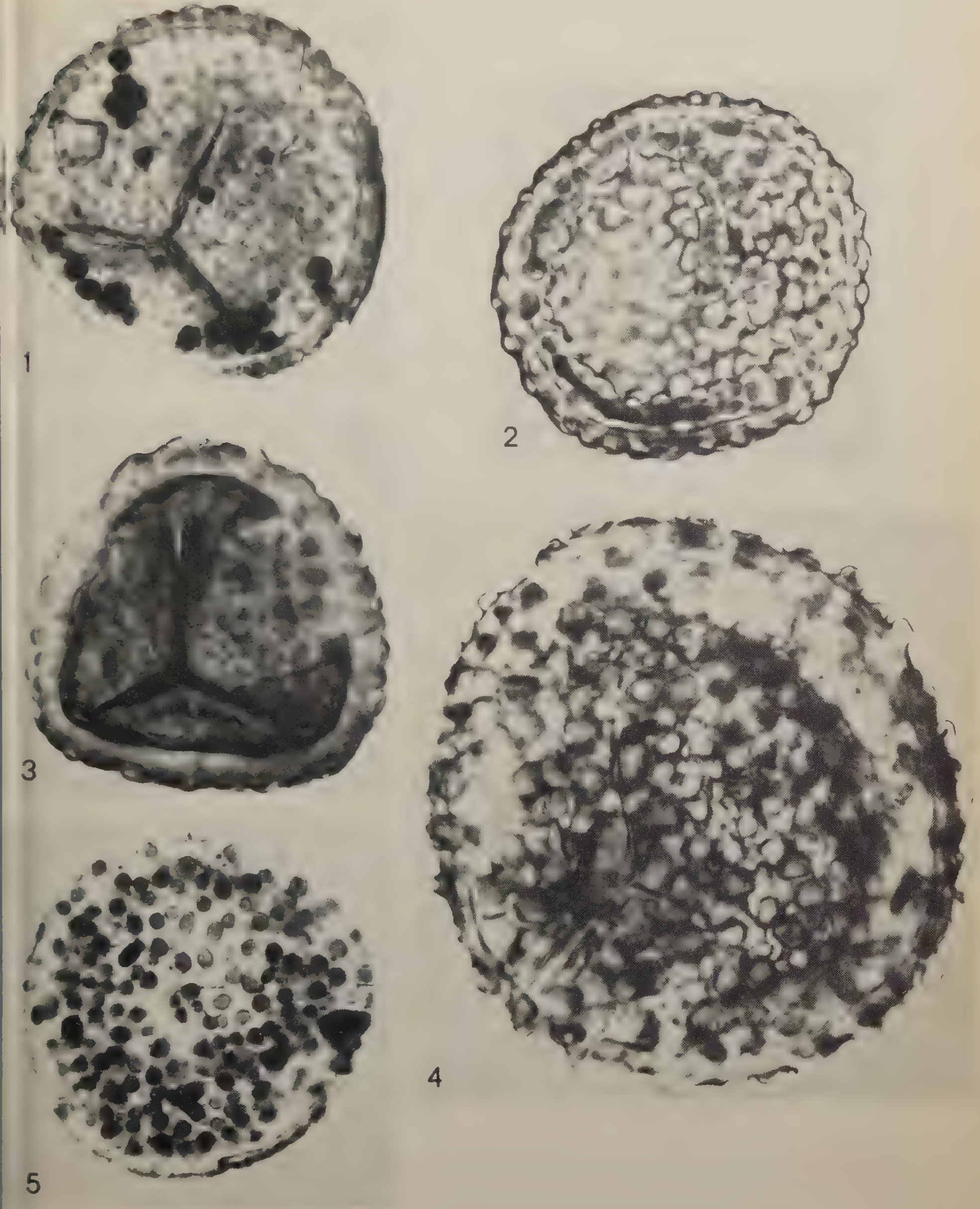


Plate I. 1. *Verrucosisporites jenensis* (675 ×); 2. id. (675 ×); 3. *Verrucosisporites reinhardtii*, holotype (675 ×); 4. *Verrucosisporites pseudomorulae*, holotype (1100 ×); 5. id. (675 ×).

PLATE I

Facing p, 350

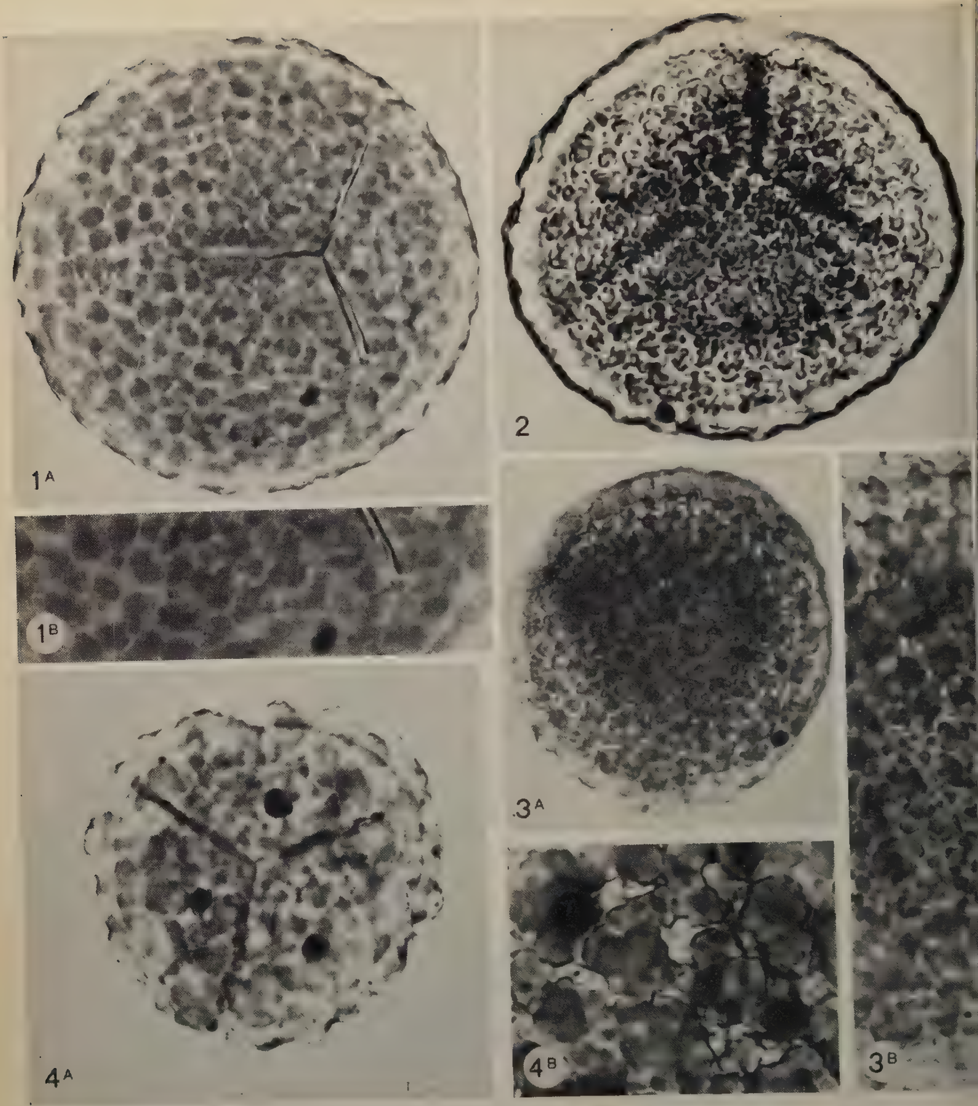


Plate II. 1A. *Guttatisporites guttatus*, holotype (650 ×); 1B. detail, showing structure; 2. *Guttatisporites microechinatus*, holotype (675 ×); 3A. id. (500 ×); 3B. detail, showing structure; 4A. *Guttatisporites elegans*, holotype (675 ×); 4B. detail, showing structure.

PLATE II

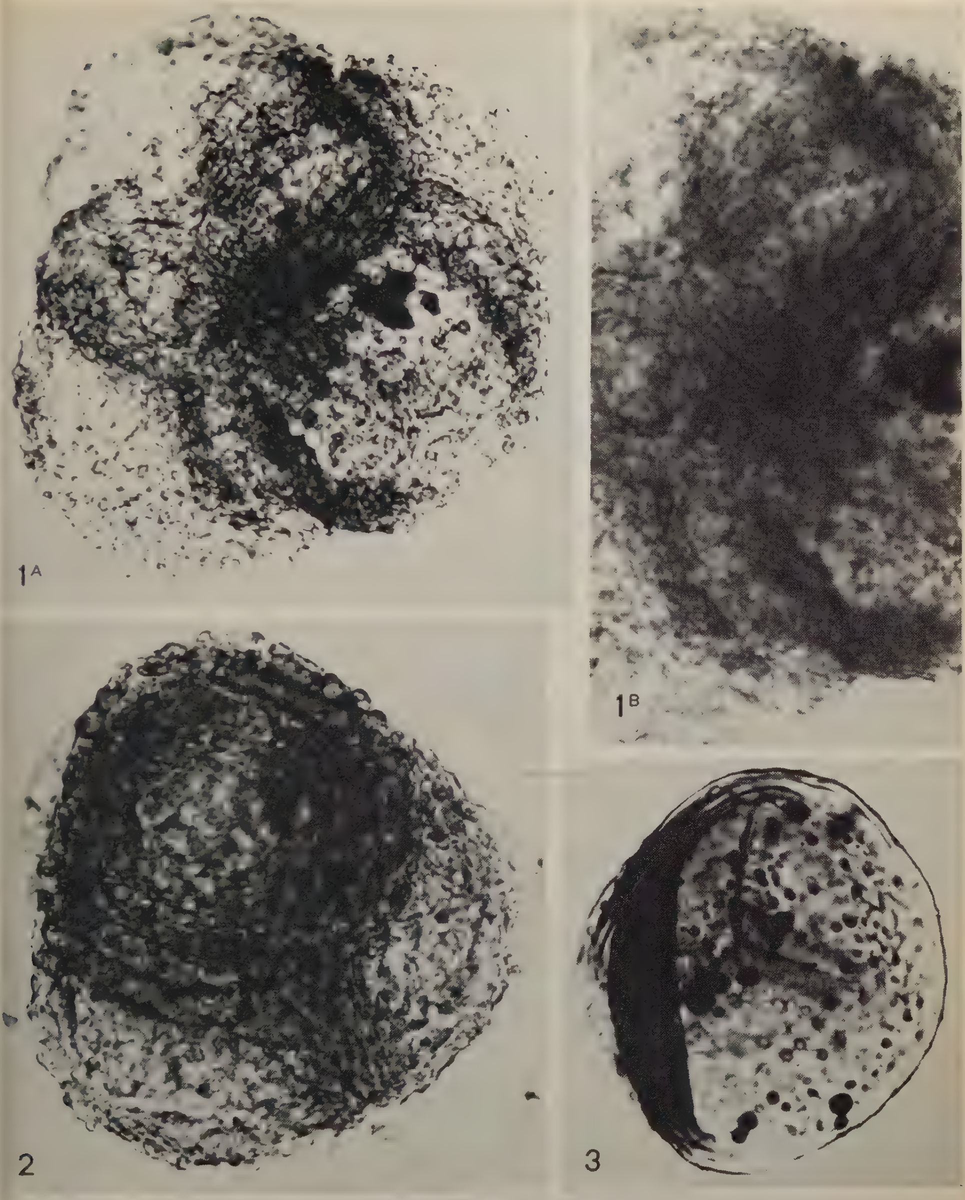


Plate III. 1A. *Lapposisporites lapposus*, holotype (800 ×); 1B. detail, showing structure; 2. id. (800 ×); 3. *Apiculatasporites plicatus*, holotype (850 ×).

PLATE III

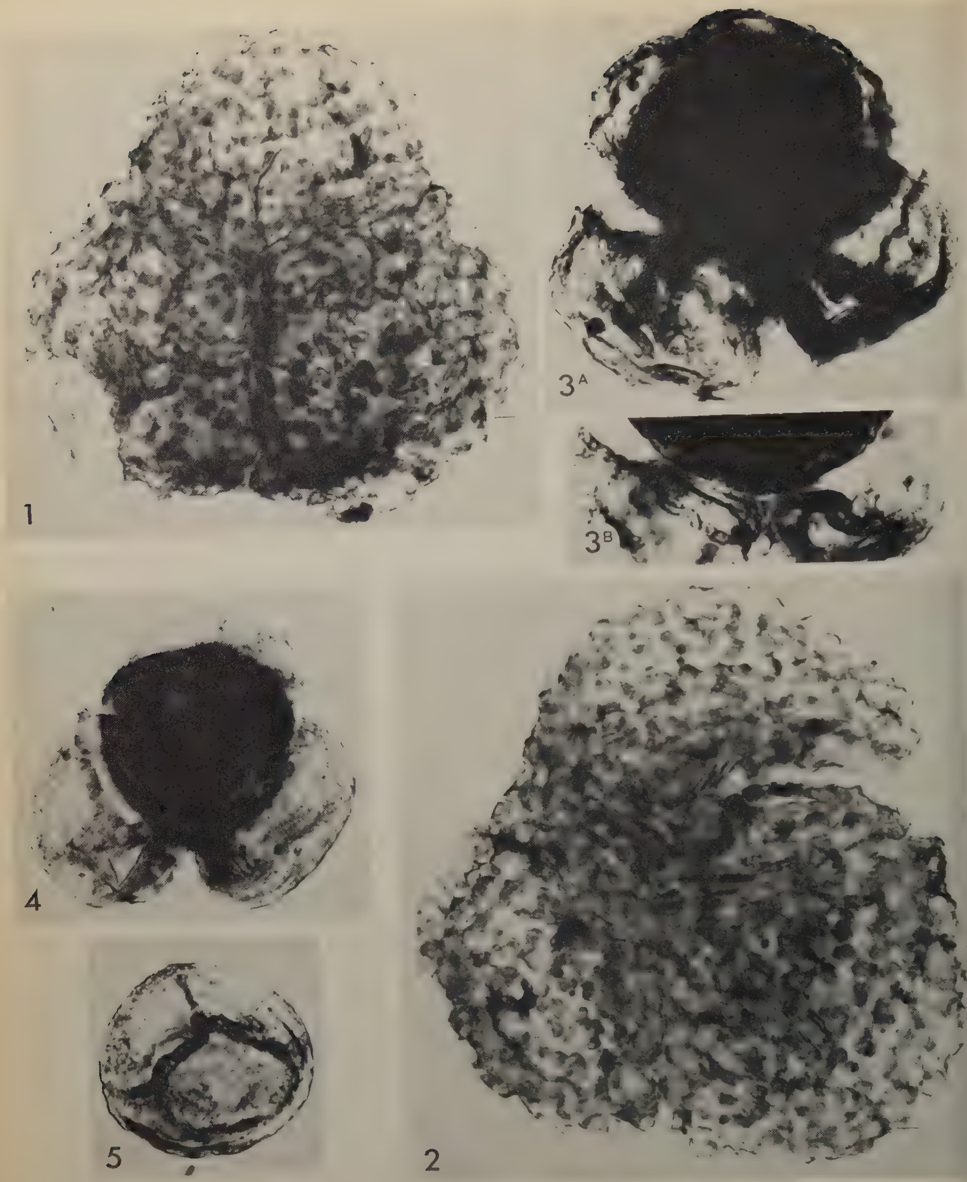


Plate IV. 1. *Lapposisporites armatus*, holotype (750 ×); 2. *Lapposisporites loricatus*, holotype (750 ×); 3A. *Paralundbladispora vieta*, holotype (800 ×); 3B. detail, showing narrow cingulum in equatorial view; 4. *Paralundbladispora quadriiuga*, holotype (800 ×); 5. id., single specimen (800 ×).

PLATE IV

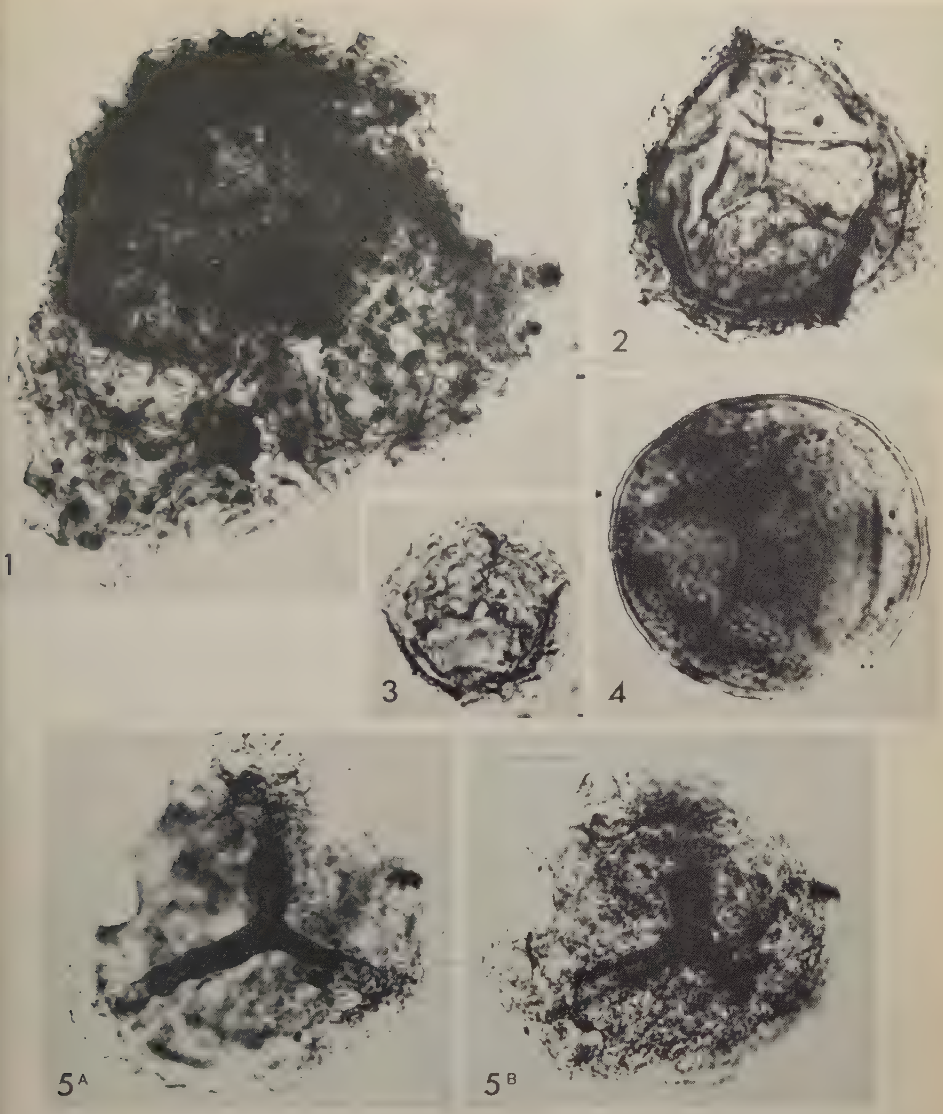


Plate V. 1. *Lapposisporites villosus*, holotype (675 ×); 2. *Densoisporites caretteae*, holotype (800 ×); 3. *Anguisporites tenuis*, holotype (800 ×); 4. *Scabratisporites scabratus*, holotype (875 ×); 5A, 5B. *Pseudogravisporites reticulatus*, holotype (800 ×).

PLATE V

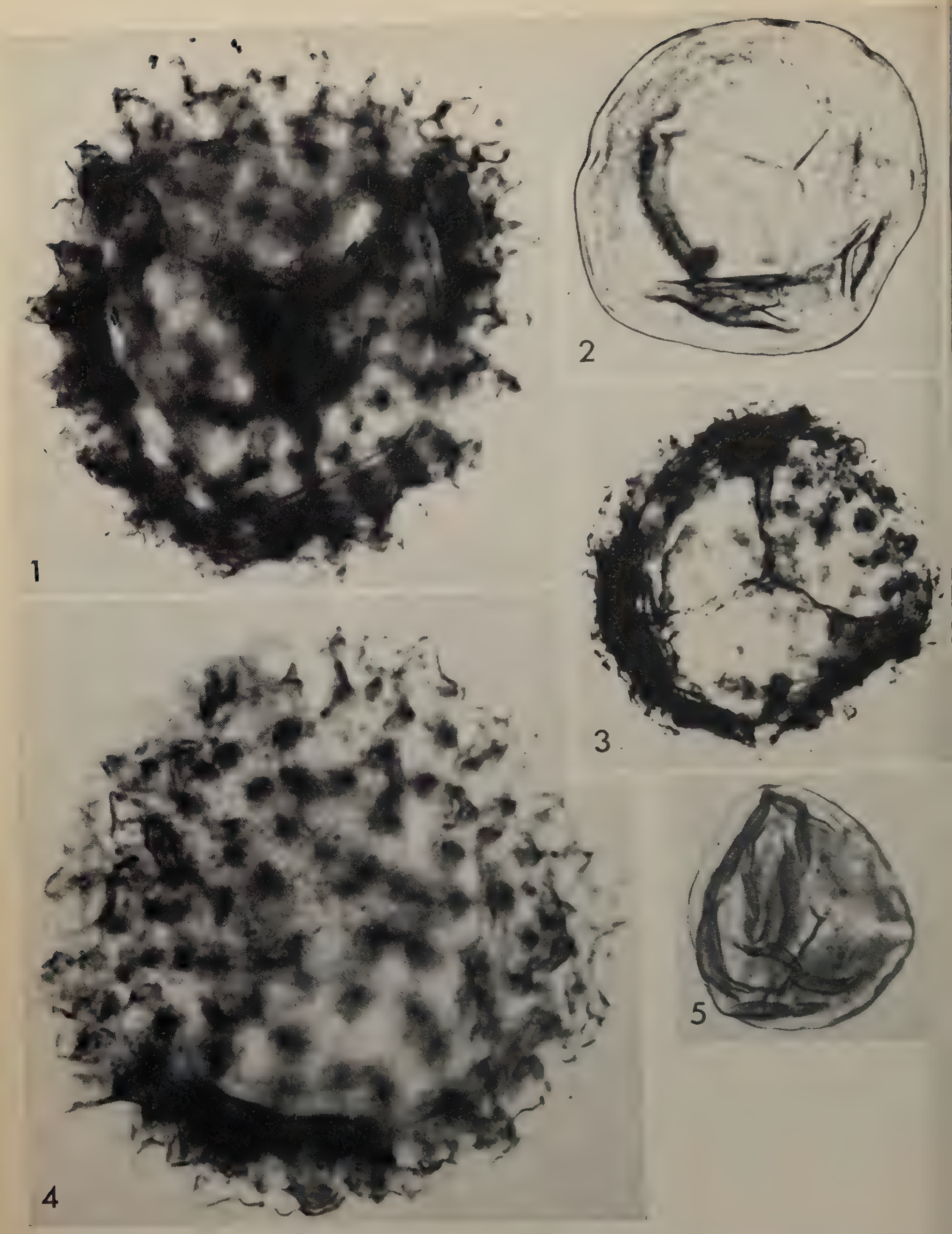


Plate VI. 1. *Kraeuselisporites hystrix*, holotype (1000 ×); 2. *Calamaspora* sp. (800 ×); 3. *Kraeuselisporites hoofddijkensis* (800 ×); 4. id., holotype (1400 ×); 5. *Psilatriletes triassicus*, holotype (750 ×).

PLATE VI

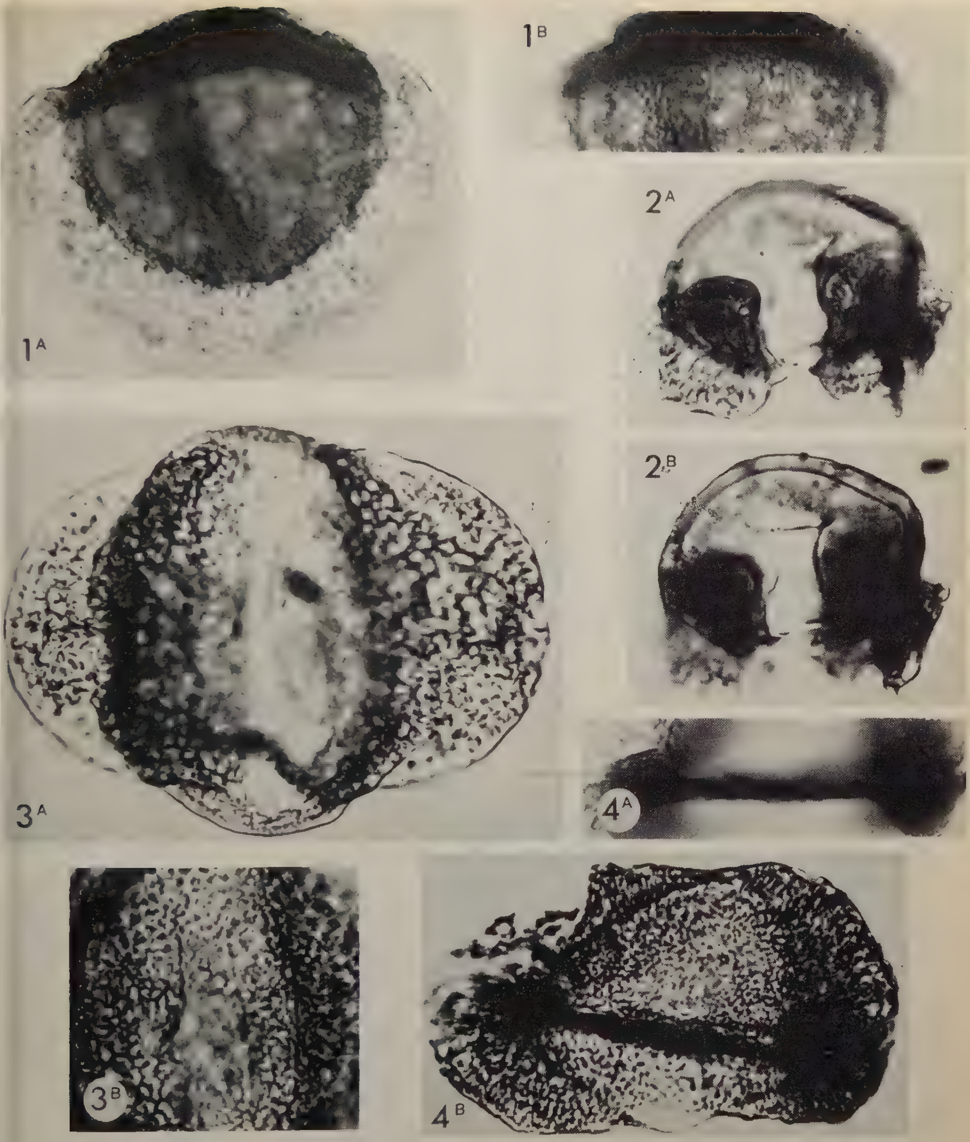


Plate VII. 1A, 1B. *Nuskoisporites inopinatus*, holotype (700 ×); 2A, 2B. *Microcachryidites doubingeri* (1000 ×); 3A, 3B. *Falcisporites snopkovae*, holotype (850 ×); 4A. *Chordasporites voltziaformis*, detail, showing chorda; 4B. id., holotype (800 ×).

PLATE VII

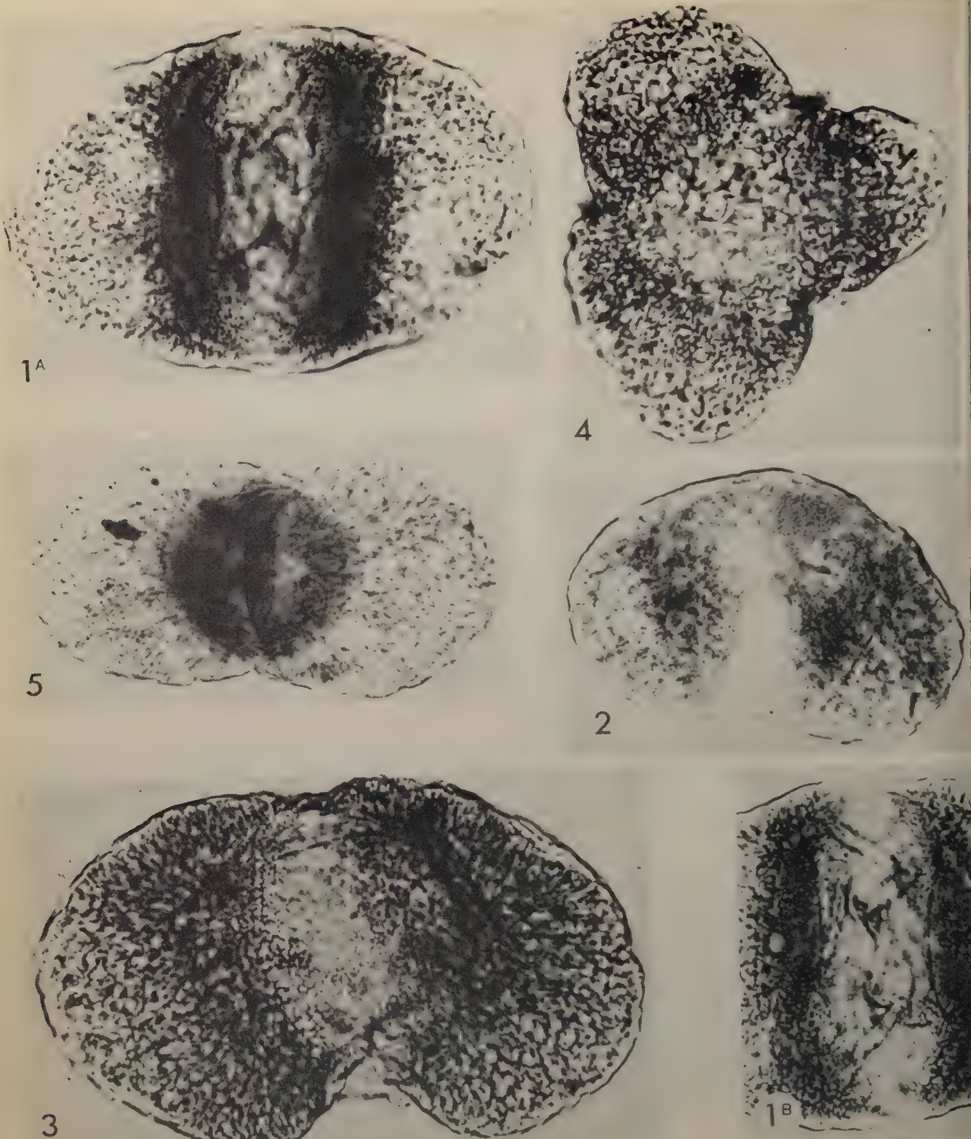


Plate VIII. 1A, 1B. *Paravesicaspora planderovae*, holotype (800 ×); 2. id., equatorial view (750 ×); 3. *Voltziaceaesporites heteromorpha* (800 ×); 4. id., trisaccate specimen (750 ×); 5. id., id., platysaccoid specimen (750 ×).

PLATE VIII

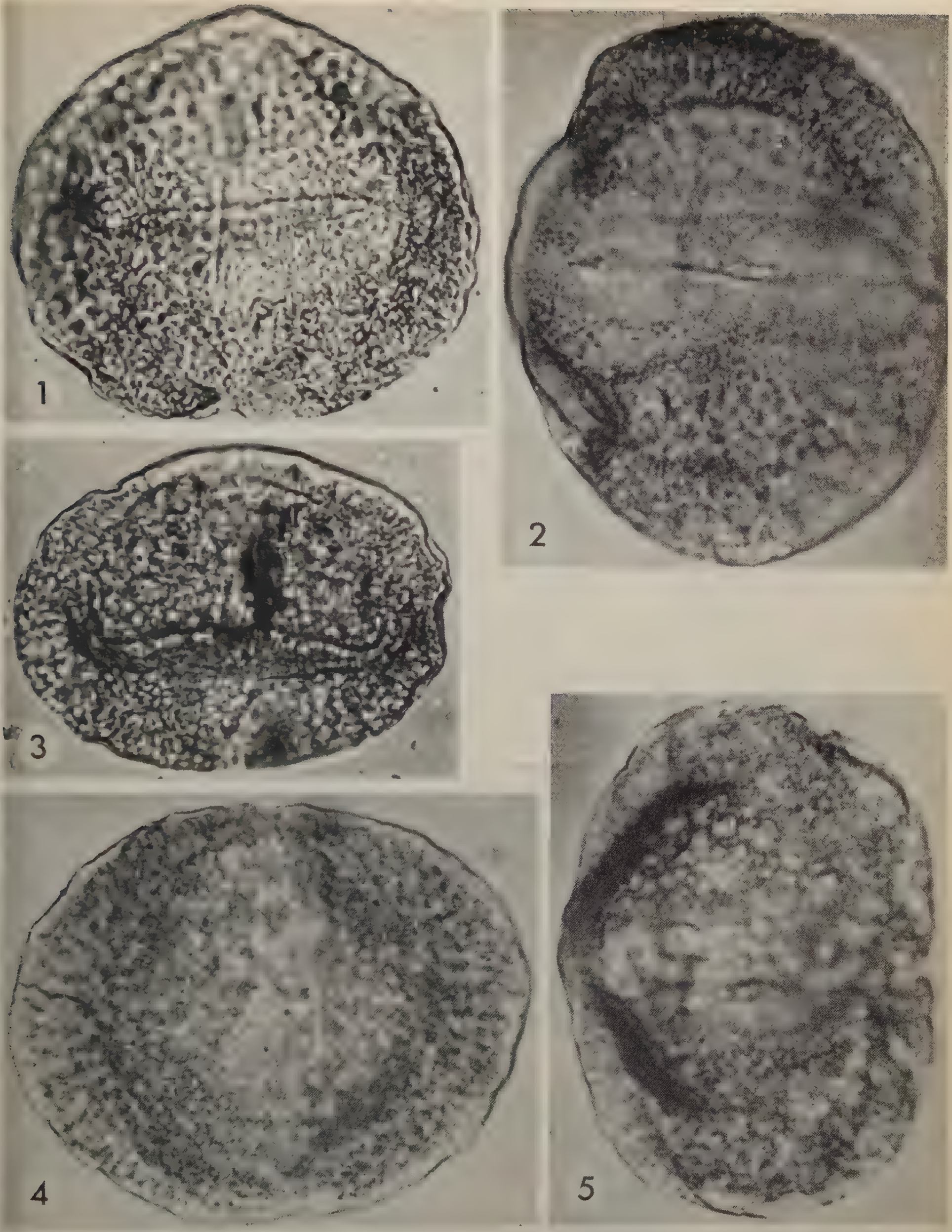


Plate IX. 1. *Colpectopollis ellipsoideus*, with distal folding; 2. id., equatorial view; 3. id., holotype, with proximal folding; 4. id., polar view without folding; 5. id., subequatorial view. (all specimens 750 ×).

PLATE IX

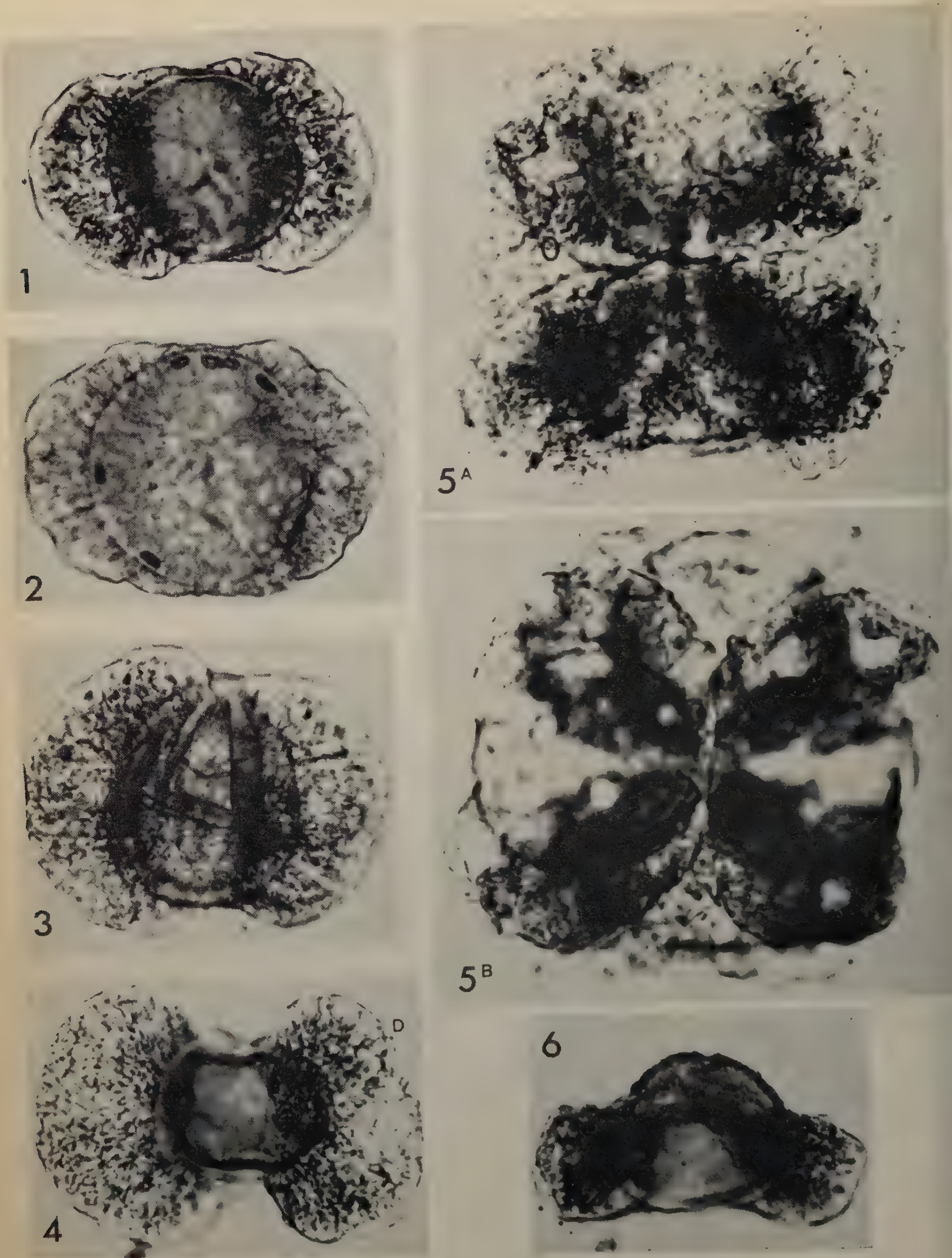


Plate X. 1. *Triadispora crassa*; 2. id.; 3. id.; 4. id., platysaccoid; 5A, 5B. id., tetrad; 6. id., equatorial view. (all specimens 750 ×).

PLATE X

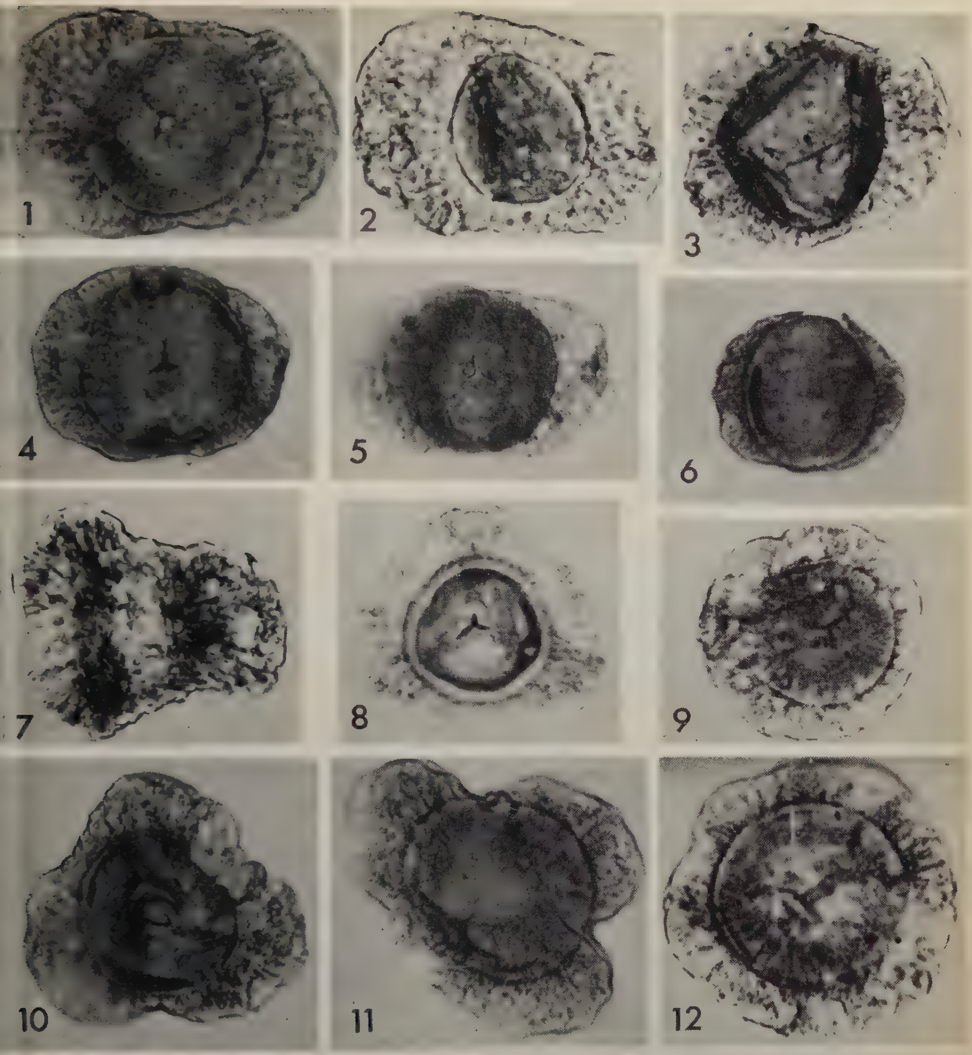


Plate XI. 1–12. *Triadispora crassa*, different shapes. (all specimens 650 ×).

PLATE XI

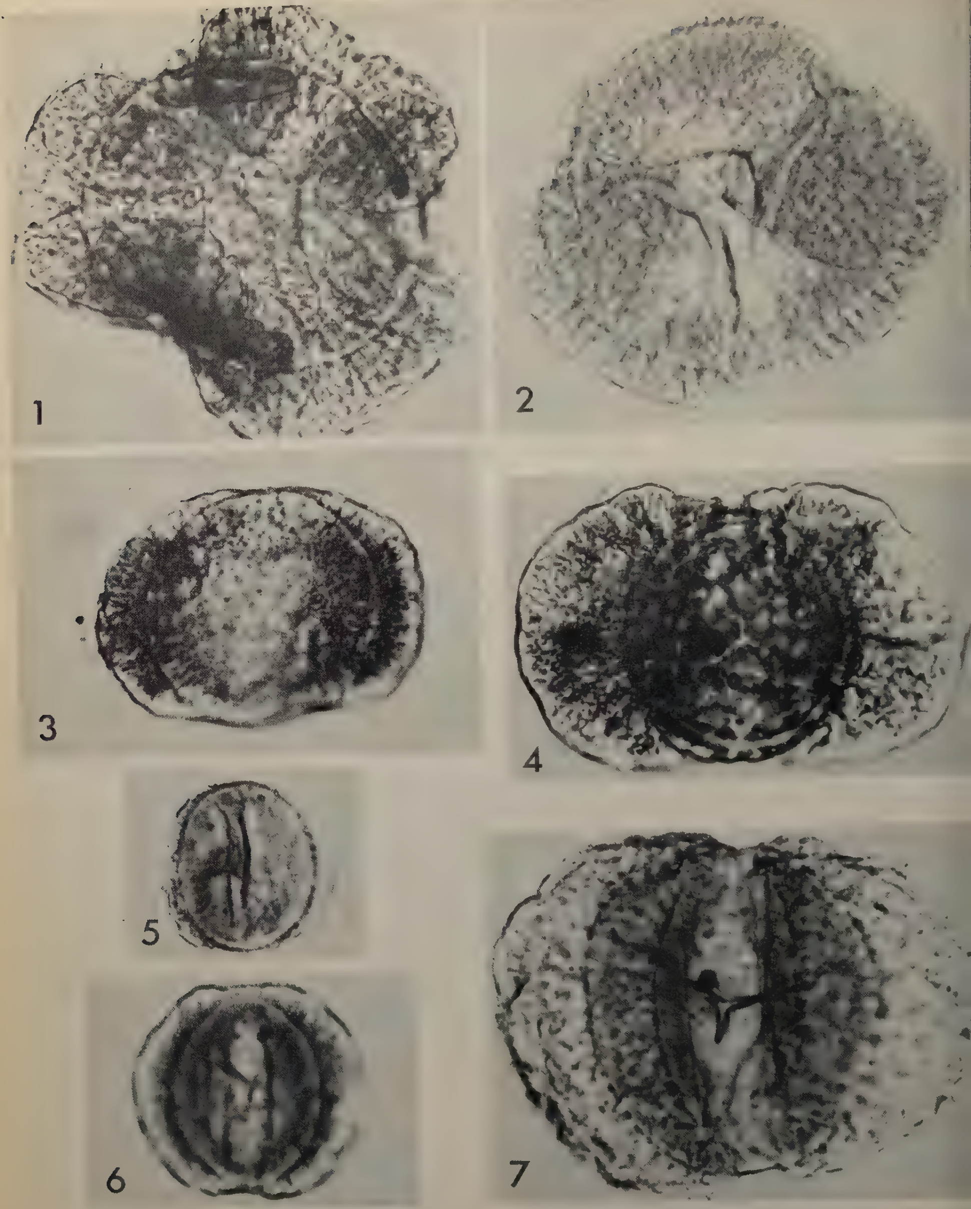


Plate XII. 1. *Triadispora muelleri*; 2. id.; 3. *Triadispora staplini*; 4. *Triadispora plicata*; 5. *Triadispora epigona*; 6. id.; 7. *Triadispora crassa*. (all specimens 750 ×).

PLATE XII

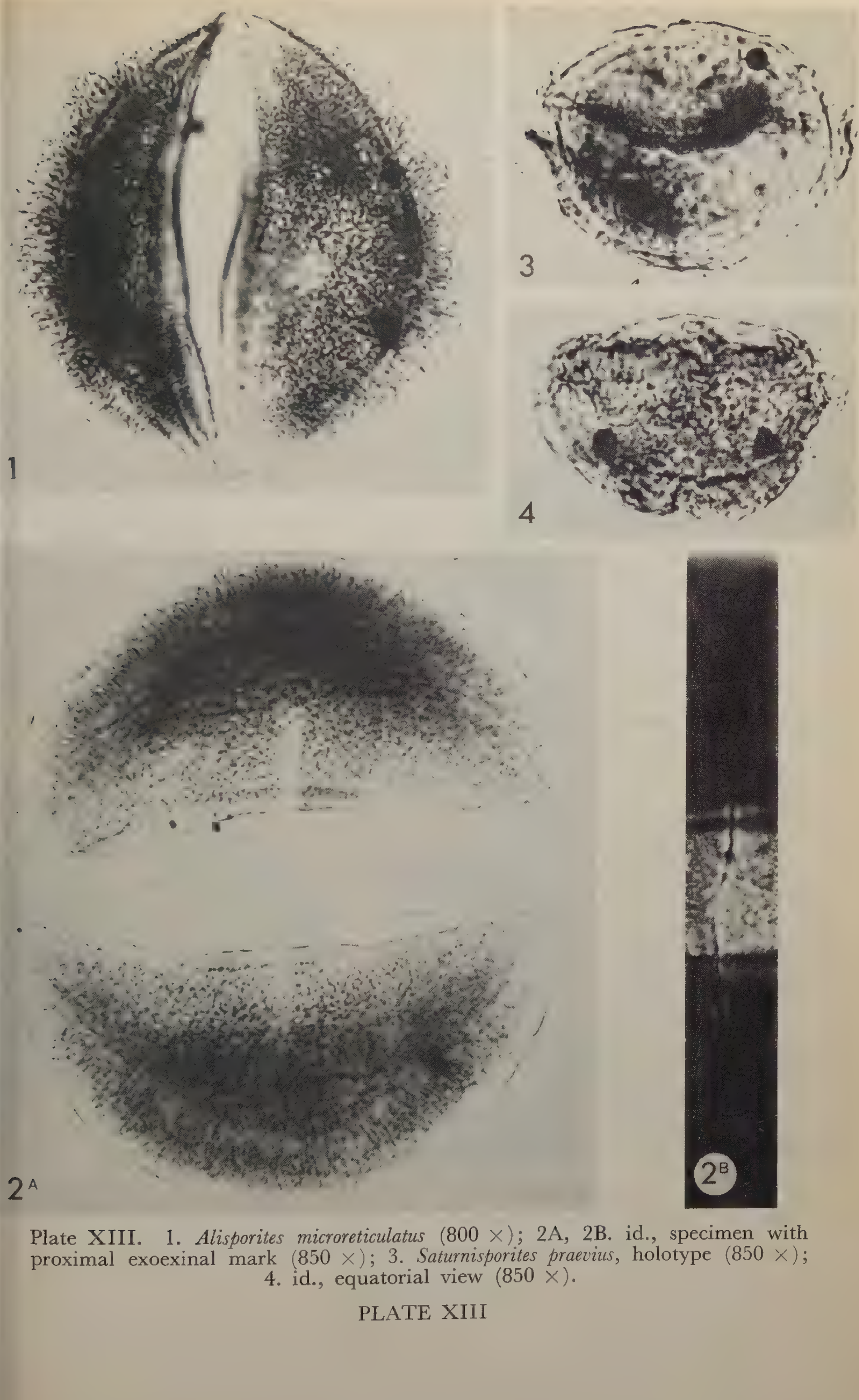


Plate XIII. 1. *Alisporites microreticulatus* (800 ×); 2A, 2B. id., specimen with proximal exoexinal mark (850 ×); 3. *Saturnisporites praevius*, holotype (850 ×); 4. id., equatorial view (850 ×).

PLATE XIII

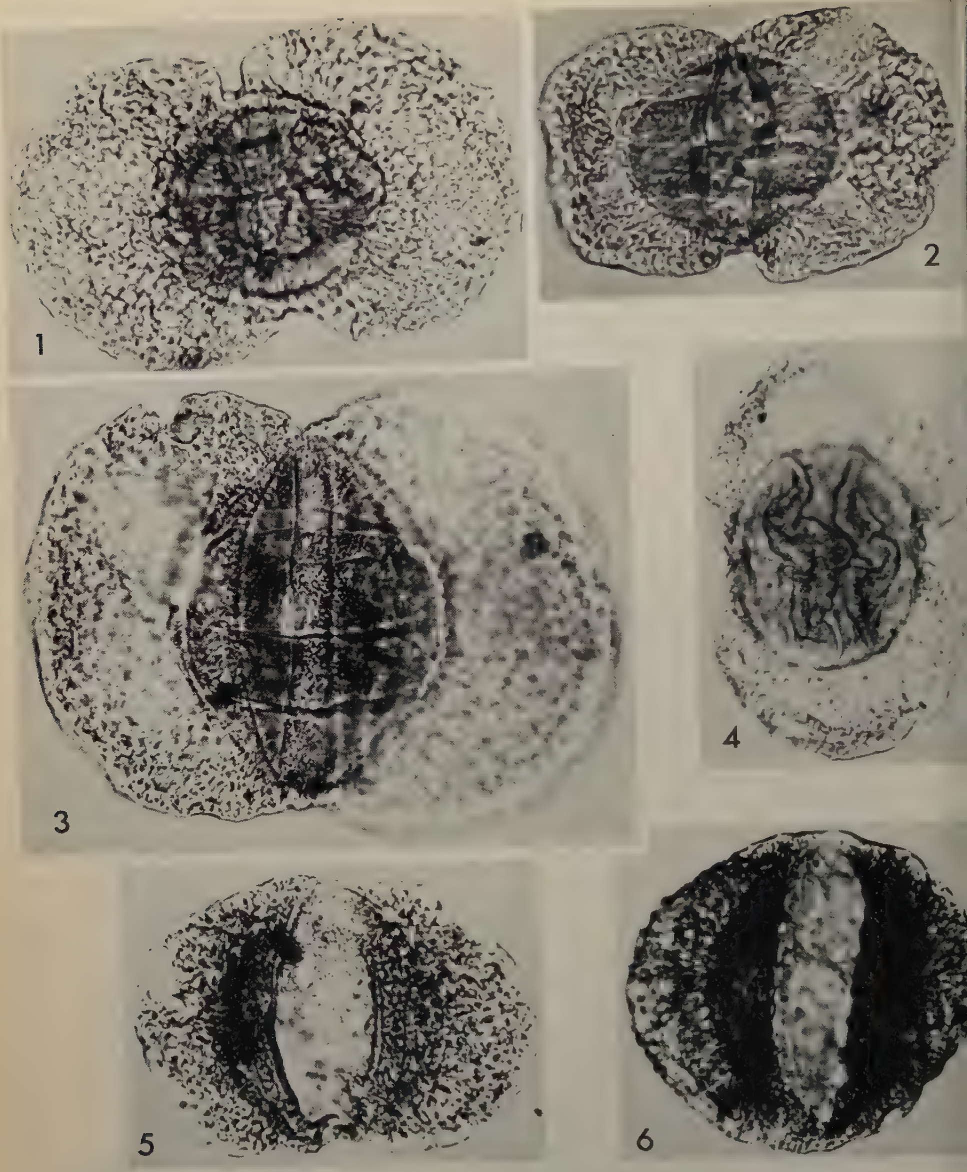


Plate XIV. 1. *Lunatisporites puntii*, platysaccoid specimen (675 ×); 2. id. (675 ×); 3. id., holotype (700 ×); 4. id., specimen with deformed taeniae (675 ×); 5. *Alisporites grauvogeli* (700 ×); 6. id. (700 ×).

PLATE XIV

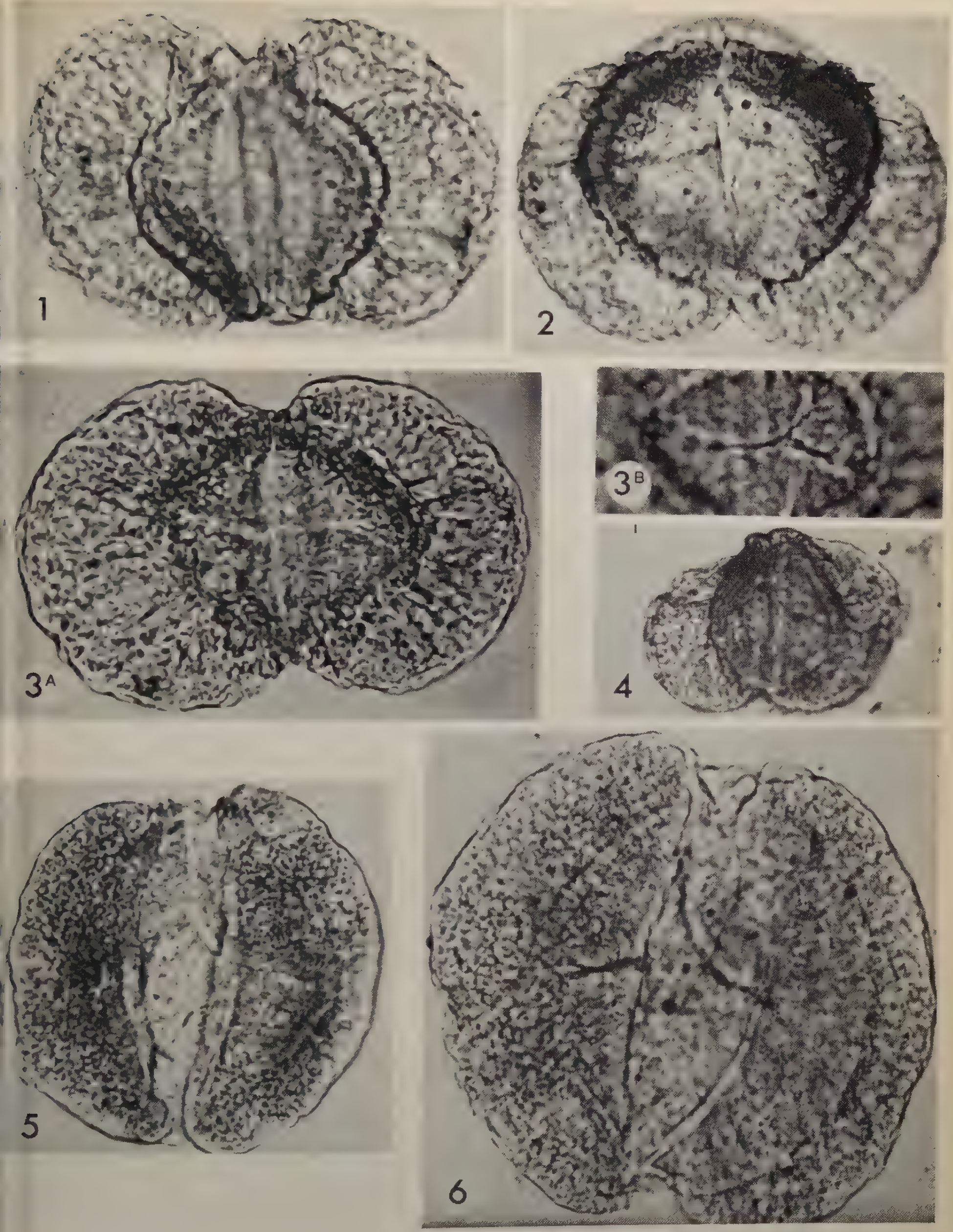


Plate XV. 1. *Angustisulcites klausii* (850 ×); 2. id., equatorial view (850 ×); 3A, 3B. id. (850 ×); 4. id., holotype described by Freudenthal 1964 (500 ×); 5. *Angustisulcites gorpii* (650 ×); 6. id., holotype (900 ×).

PLATE XV

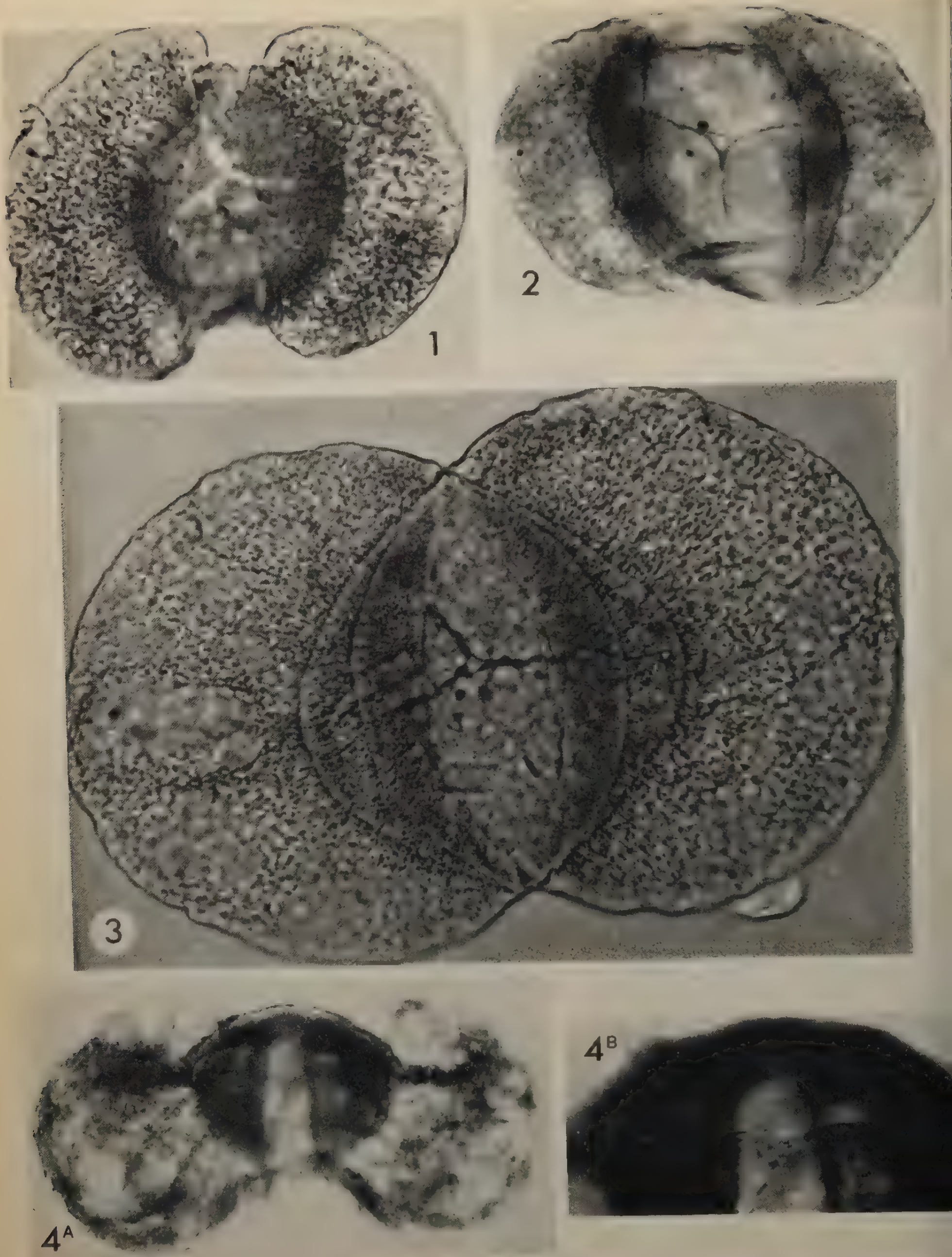


Plate XVI. 1. *Angustisulcites gorpii* (750 ×); 2. *Illinites trivisus*, holotype (750 ×); 3. *Angustisulcites grandis* (750 ×); 4A. id., equatorial view (350 ×); 4B. detail, showing equatorial suture.

PLATE XVI

and *T. muelleri*. As stratigraphical counter-arguments are lacking also monosaccate and platysaccoid forms are placed within *T. crassa*.

The presence of transveral folding has to be considered a secondary feature; both forms with one and with two folds can be found, but also folds in other directions appear frequently. However, the haploxylonoid *T. falcata* and its transitions may be more sensitive to compression folding.

Apart from the shape of the sacci there are also variations in size, Y-mark development (trilete, reduced trilete, rarely monolete), distal bladder base (distinct or indistinct) and proximal exoexinal structure of cental body (tendency to plicate structure which results in *T. plicata*).

Klaus (1964) mentioned already the occurrence of tetrads; Plate X, Figs. 5A, B shows a well preserved example of *T. crassa* quadruplets.

Table 7

The variation within the genus *Triadispora* (mean percentages of some important forms)

shape	species	mean (%)
haploxylonoid	*T. staplini*	4
diploxylonoid	*T. crassa*	66
submonosaccate/monosaccate	*T. crassa*	12
transversal folds	mainly *T. crassa*	2
subtrisaccate/trisaccate	*T. crassa*/*T. muelleri*	4
reduced sacci	*T. epigona*	7
plicate	mainly *T. plicata*	2
"*Falcisporites*-like"	*T. falcata*	1

Table 7 shows the averages of the most prominent forms of *Triadispora* in the Hengelo assemblage. The remainder mainly consists of badly preserved indeterminable specimens, which mostly show lost sacci or a dissolved intexine. Also Klaus (1964) reported the frequency of the latter phenomenon.

Occurrence: *T. crassa* is common in the Hengelo Röt salinar. In the upper part of the Röt pelites the species is less frequent. Klaus (1964) reported *T. crassa* from the Vosges and from Thüringen.

Triadispora staplini Klaus 1964

Fig. 22c; Plate XII, Fig. 3.

Holotype: *Triadispora staplini* Klaus 1964, t. 1, f. 5 (non *Klausipollenites staplini* Jansonius 1962, t. 12, f. 21).

Remarks and comparisons: Klaus (1964) stated that the haploxylonoid forms of *Triadispora* should be identical with *Klausipollenites staplini* Jansonius 1962. Some of Jansonius' Canadian preparations, rich in *K. staplini*, are stored in Utrecht and the author restudied this species. He disagrees with Klaus' conception about its fundamental trilete character. In some rare cases faint lines may suggest an Y-mark, but probably these are secondary phenomena. Furthermore the species possesses the characteristic thickened bladder base, already reported by Jansonius (1962). Because of the alete character the Canadian species cannot be placed within the genus *Triadispora*. So with regard to the European haploxylonoid *Triadispora*-forms the epithet *staplini* and Klaus' specific diagnosis remain useful. A new holotype has been chosen from Klaus' illustrations (Klaus 1964, t. 1, f. 5).

The position of *Falcisporites staplini* (Jansonius 1962) Freudenthal 1964 is not clear. Freudenthal does not illustrate this species and single grain slides are unavailable.

Only truly haploxylonoid forms without equatorial bladder interconnections are considered as *T. staplini*; for practical reasons transitions to *T. crassa* are considered as the latter species. Specimens with very small haploxylonoid sacci belong to *T. epigona*; in this case the transitions are considered as *T. staplini*. Transitions to *T. plicata* have not been recognized.

Occurrence: Very low percentages in the Hengelo Röt salinar; very frequent in the German, French, Italian and Austrian Upper Bunter assemblages investigated by Klaus (1964).

Triadispora falcata Klaus 1964

Fig. 22f.

Holotype: *Triadispora falcata* Klaus 1964, t. 1, f. 6.

Remarks and comparisons: Triadispora-forms conforming to the description of *T. falcata* have been demonstrated very seldom in the Hengelo assemblage. Well preserved specimens for using in single grain slides have not been found.

The presence of transversal folds is considered a secondary phenomenon (p. 351). However, the haploxylonoid *Falcisporites*-like sacci are sufficiently characteristic to maintain *T. falcata*. Transitions to *T. crassa* occur less seldom; they are considered as the latter species (Freudenthal 1964, t. 1, f. 1: "*Eridospollenites bentzi*").

Occurrence: Very rare in the Hengelo Röt salinar. Klaus (1964) also recognized the species in Upper Bunter assemblages.

Triadispora muelleri (Reinhardt and Schmitz in Reinhardt 1964b) nov. comb.

Fig. 22e; Plate XII, Figs. 1, 2.

Holotype: *Triadispora* (al. *Nuskoisporites*) *muelleri* (Reinhardt and Schmitz in Reinhardt 1964b) nov. comb.; Reinhardt 1964b, t. 1, f. 5.

Remarks and comparisons: Unlike Reinhardt (1964b) we consider *T. muelleri* a fundamentally trisaccate species. Via transitions it can be derived from *T. crassa* (Fig. 22). *T. muelleri* differs from these transitional forms by its relatively bigger central body, by the less projecting oval sacci (in polar view), by the rather distinct bladder bases and by the very characteristic distal bladder interconnections. Although trisaccate the species has been placed within a bisaccate genus. By creating a new trisaccate genus the relation with *T. crassa* would not be clear. *Nuskoisporites* is limited to monosaccate species; consequently the characteristic shape of the germinal of *T. muelleri* is absent.

Occurrence: Hengelo Röt salinar and upper Röt pelites; rare. Reinhardt (1964b) mentioned the species from the Lower Röt of Thüringen.

Triadispora plicata Klaus 1964

Fig. 22b; Plate XII, Fig. 4.

Holotype: *Triadispora plicata* Klaus 1964, t. 2, f. 15.

Remarks and comparisons: Although connected with *T. crassa* by transitions, we consider forms with a clearly plicate central body and thickened proximal exoexine as *T. plicata.* Transitions to haploxylonoid forms (*T. staplini*) and to forms with reduced sacci (*T. epigona*) have not been demonstrated.

Occurrence: Hengelo Röt salinar; rare. Klaus (1964) reports the species from Italian and French Muschelkalk assemblages; here it is more frequent.

Triadispora epigona Klaus 1964

Fig. 22d; Plate XII, Figs. 5, 6.

Holotype: *Triadispora epigona* Klaus 1964, t. 2, f. 13.

Remarks and comparisons: Although connected with *T. crassa* and *T. staplini* by transitions, we maintain *T. epigona* for stratigraphical reasons (p. 326). It differs from the former species by its small reduced sacci. These can be haploxylonoid or faintly diploxylonoid with a semi-lunar shape. But also forms with a small monosaccus are rather frequent. Depending on the saccus shape, the transitions are placed within *T. crassa* or *T. staplini.*

Occurrence: Regularly recognized in the Hengelo Röt Group; never in high percentages. Klaus (1964) mentions the species from French and Italian Muschelkalk assemblages; sometimes rather dominant.

INFRATURMA *Striatiti* Pant 1954

SUBINFRATURMA *Aletestriatiti* nov. subinfraturma

Diagnosis: Pollen bisaccate, striate. Intexine of the central body without proximal tetrad mark.

Remarks: The author considers the presence or absence of an intexinal tetrad mark within the *Striatiti* a very important feature. It seems a good argument for subdividing the *Striatiti* into the *Aletestriatiti* nov. subinfraturma and the *Triletestriatiti* nov. subinfraturma (p. 360).

Illinites Kosanke 1950 emend. Klaus 1964

Type species: *Illinites unicus* Kosanke 1950, t. 1, f. 3.

Remarks and comparisons: By restudying the type specimen both Jansonius and Staplin (1962) and Klaus (1964) have given valuable contributions to a better knowledge of the genus *Illinites* (synonym: *Complexisporites* Jizba 1962). By the proximal exoexinal differentiations (reduced trilete mark accompanied by two laterally placed longitudinal sutures) *Illinites* can be distinguished from the "*Illinites*"-species from the European Upper Permian (≡ *Eridospollenites* Freudenthal 1964, which has to be considered, together with *Jugasporites* Leschik 1956b, as *Limitisporites* Leschik 1956b emend. Potonié 1958 (the genus *Jugasporites* Leschik 1956b emend. Klaus 1963a might be preferable, but according to Art. 57 of the International Code of Botanical Nomenclature Potonié's "choice must be followed"). An intexinal (reduced) trilete or monolete is absent.

Illinites differs from *Angustisulcites* Freudenthal 1964 emend. by possessing approx. haploxylonoid sacci and by the still proximal, not equatorially placed longitudinal sutures. Both genera are related more to the *Striatiti* Pant 1954 than to the *Disaccitriletes* Leschik 1956. So we place both genera in the former infraturma.

Illinites trivisus n. sp.

Fig. 23; Plate XVI, Fig. 2.

Holotype: *Illinites trivisus* n. sp. Single grain slide 31-HV-271; Plate XVI, Fig. 2.

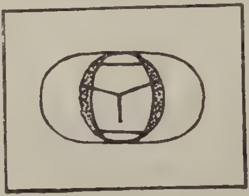


Fig. 23. *Illinites trivisus*

Diagnosis: Pollen bisaccate, striate. Equator of central body approx. circular to transversely elliptical. Exine with fine infrastructure. Trilete mark in proximal exoexine well developed: two rays extend to the equator, the third – transversal – ray is hardly reduced. This Y-mark is accompanied by two still proximally situated longitudinal sutures. Proximal intexine without (reduced) trilete or monolete mark. Sacci finely infrareticulate, approx. haploxylonoid with narrow equatorial interconnections. Bladder bases usually accompanied by folds. Known size range 70–80 μ (holotype 78 μ).

Comparison: Illinites kosankei Klaus 1964, also from Upper Bunter assemblages, differs by possessing a strongly reduced Y-mark and by its bigger size.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).

Occurrence: Only recognized in the shales between 405.50 and 406.80 m; rare.

Angustisulcites Freudenthal 1964 emend.

Type species: *Angustisulcites klausii* Freudenthal 1964, t. 2, f. 6a, 6b; Plate XV, fig. 4.

Diagnosis: Pollen bisaccate, striate. Equator of central body approx. circular to transversely elliptical or, very often, subangular (rhombic). Proximally thickened exoexine with Y-mark; two rays extend to the equator, the third may be strongly reduced and assymmetrically placed. Apart from the Y-mark there are two equatorially situated longitudinal exoexinal sutures. Consequently these are only visible in equatorial view (lateral view). Proximal intexine without (reduced) trilete or monolete mark. Sacci faintly diploxylonoid to strongly libelloid. In principle the distal germinal area is biconvex; it is often accompanied by transversal compression folds.

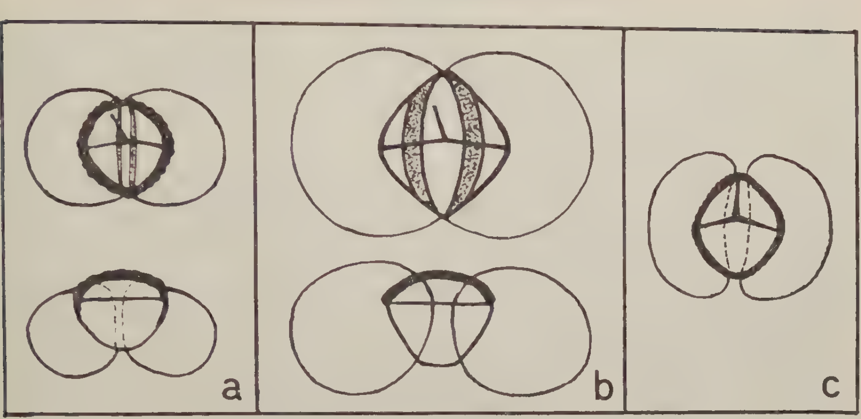


Fig. 24. *Angustisulcites.* a. *A. klausii*; b. *A. grandis*; c. *A. gorpii*

Remarks and comparisons: FREUDENTHAL (1964) based his generic diagnosis on a badly preserved type specimen which does not show a distinct Y-mark in the proximal exoexine. We reprepared the genotype and have been able to demonstrate the Y-mark. Specimens without a distinct open mark have also been found in our preparations, but usually it becomes visible with high magnification. In order to include more species we changed Freudenthal's generic description in a more extensive sense; not even to *Angustisulcites klausii* Freudenthal 1964 can the "narrow deep sulcus" be considered characteristic. *Angustisulcites* is highly related to *Illinites* Kosanke emend. Klaus 1964; it differs by the diploxylonoid shape, but especially by the equatorial position of the lateral sutures, which are invisible in polar view (proximo-distal view).

Angustisulcites differs from *Lueckisporites* Potonié and Klaus 1954 emend. Klaus 1963a by the trilete shape of the proximal exoexinal mark and by the absence of a monolete or (reduced) trilete mark in the proximal intexine. The latter fact has been the argument for placing *Angustisulcites*, together with *Illinites*, within the *Aletestriatiti* nov. subinfraturma.

Angustisulcites klausii Freudenthal 1964

Fig. 24a; Plate XV, Figs. 1, 2, 3A, B, 4.

Holotype: *Angustisulcites klausii* Freudenthal 1964, t. 2, f. 6a, 6b; Plate XV, Fig. 4.

Diagnosis: Pollen bisaccate, striate. Equator of central body circular, transversely elliptical or subangular (rhombic). Strongly thickened proximal exoexine (3–4.5 μ) with fine infrastructure and trile mark; two rays extend to the equator, the third ray can be strongly reduced and is placed asymmetrically. Equatorially two longitudinal singular exoexinal sutures, only visible in equatorial view. Intexine without (reduced) trilete or monolete mark. Sacci faintly diploxylonoid, distally inclined, laterally close to each other or equatorially interconnected by a narrow exoexinal strip. Distal germinal area fundamentally biconvex; usually accompanied by transversal folds. Observed size range 57–85 μ.

Remarks and comparisons: By restudying the holotype we have been able to demonstrate the exoexinal Y-mark (p. 355). Although narrow germinal areas appear very frequently, a "narrow deep sulcus" (Freudenthal 1964) cannot be considered characteristic; a variation from 1–7 μ was recognized.

A. klausii is very close to *Illinites melanocorpus* Klaus 1964; it only differs by its smaller average size (respectively 57–85 μ and 90–120 μ). Further investigations have to show whether *I. melanocorpus* can be maintained for stratigraphical reasons.

Angustisulcites gorpii n. sp. distinguishes by its libelloid shape, its unreduced transversal trilete ray and by possessing a very characteristic saccus infrareticulum. *Angustisulcites grandis* (Freudenthal 1964) nov. comb. differs by its striking size.

Occurrence: Regularly recognized in the Röt salinar of Hengelo; low percentages. In the upper part of the overlying Röt pelites, however, *A. klausii* is the most dominating species.

Angustisulcites grandis (Freudenthal) 1964 nov. comb.

Fig. 24b; Plate XVI, Figs. 3, 4A, B; Plate XVII, Figs. 1, 2.

Holotype: *Angustisulcites* (al. *Falcisporites*) *grandis* (Freudenthal 1964) nov. comb.; Freudenthal 1964, t. 5, f. 1.

Diagnosis: Pollen bisaccate, striate. Striking but variable size (known size range 110–210 μ). Equator of central body approx. circular to strongly subangular (rhombic). Thickened proximal exoexine with reduced trilete mark; two rays extend to the equator, the third – approx. transversal – is reduced and situated asymmetrically. Equatorially two longitudinal singular exoexinal sutures, only visible in equatorial view. These sutures also limit the thickened proximal exoexine, Proximal intexine without (reduced) trilete or monolete mark. Sacci faintly to strongly diploxylonoid, both proximally and distally inclined, laterally close to each other or equatorially interconnected. Fine, more or less imperfect, saccus-infrareticulum. Distal germinal area fundamentally biconvex, usually accompanied by folds.

Remarks and comparisons: Especially the bigger specimens are usually badly preserved. This also applies to Freudenthal's holotype. Even with high magnification a trilete mark can be suspected only. On account of the general shape and of analogue finds within the variation of a trilete species Freudenthal's specimen has to be maintained as the holotype of *Angustisulcites grandis* (Freudenthal 1964) nov. comb. Our better preserved specimens explain the upbuilding of *A. grandis* which differs from *Angustisulcites klausii* Freudenthal 1964 and *Angustisulcites gorpii* n. sp. by its striking size.

Occurrence: Regularly recognized in the Hengelo Röt salinar; never in high percentages.

Angustisulcites gorpii n. sp.

Fig. 24c; Plate XV, Figs. 5, 6; Plate XVI, Fig. 1.

Holotype: *Angustisulcites gorpii* n. sp. Single grain slide 31-HV-226; Plate XV, Fig. 6.

Derivatio nominis: J. J. M. van Gorp, chemist in Tilburg, the Netherlands, who gave valuable chemical advices during our investigations.

Diagnosis: Pollen bisaccate, striate. Equator of central body transversely elliptical to subangular (rhombic). Strongly thickened exoexine with trilete mark; two rays always extend to the equator, the third – approx. transversal – ray can also reach the equator or can be slightly reduced; this ray is approx. symmetrically situated. Equatorially two longitudinal singular exoexinal sutures, only visible in equatorial view. The suture situated at the side, to which the transversal trilete ray extends has developed only rudimentalary. Proximal intexine without (reduced) trilete or monolete mark. Sacci libelloid, distally inclined, laterally close to each other. Striking infrareticulum with narrow elongated meshes. Distal germinal area fundamentally biconvex. Known size range 65–95 μ (holotype 78 μ).

Remarks and comparisons: Because of the strongly libelloid shape equatorially flattened specimens are very rare; it has been impossible to find a well-preserved specimen that lent itself to illustrate the equatorial sutures. They can often be vaguely observed in approximately polar view.

A. gorpii differs from *Angustisulcites klausii* Freudenthal 1964 and *Angustisulcites grandis* (Freudenthal 1964) nov. comb. by its well-developed transversal trilete ray, the libelloid shape and the characteristic saccus infrareticulum.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).

Occurrence: Regularly recognized in the Röt salinar of Hengelo; never in high percentages.

Lunatisporites Leschik 1956a emend. Bharadwaj 1962

Type species: *Lunatisporites acutus* Leschik 1956a, t. 7, f. 24.

Remarks and comparisons: By many authors (Grebe 1957; Klaus 1960; Bharadwaj 1962; Jansonius 1962; Hart 1964; Freudenthal 1964) the type species of *Lunatisporites* Leschik 1956a and *Taeniaesporites* Leschik 1956a (respectively *Lunatisporites acutus* Leschik 1956a and *Taeniaesporites kraeuseli* Leschik 1956a) are considered identical; in this case both genera have to be united. We agree with this conception. However, in the literature there is no unanimity about the question of taxonomical priority, which is given to *Lunatisporites* as well to *Taeniaesporites*.

Leschik (1956a) described both genera in the same paper; *Lunatisporites* at p. 56, *Taeniaesporites* at p. 58. The descriptions are poor and insufficient.

Grebe (1957) restudied the type species and did not notice any important differences. However, she united both genera with *Lueckisporites* Potonié & Klaus 1954.

Leschik (1959) disagrees with Grebe's concept about the nature of the semi-lunar dark area on the central body of *Lunatisporites*; this should be a morphological feature instead of an optical effect.

Klaus (1960) followed Grebe (1957).

Bharadwaj (Febr. 1962) states that there are no differences between the two genera. On account of "page priority" he considers *Taeniae-*

sporites a synonym of *Lunatisporites* Leschik 1956a emend. Bharadwaj 1962. Independently, Jansonius (April 1962) stated the same concept. But because of the better preserved holotype he gives priority to *Taeniaesporites* Leschik 1956a emend. Jansonius 1962.

Klaus (1963a) disagrees, since according to the "page priority" *Lunatisporites* should have been chosen. He appeals to Leschik (1959) in order to maintain a separation between *Lunatisporites* and *Taeniaesporites* Leschik 1956a emend. Klaus 1963a.

Hart (1964) also considers the type species identical, but next he argues inconsistently by maintaining *Taeniaesporites* without mentioning *Lunatisporites* as a synonym. The latter genus can be found in the list of synonyms of the genus *Protohaploxypinus* Samoilovich 1953 emend. Hart 1964.

Freudenthal (1964) follows Jansonius (1962).

Jansonius has been perfectly correct and logical in choosing *Taeniaesporites*. Bharadwaj was guided by the "page priority" when he chose *Lunatisporites*. On the other hand, this "page priority" has been the very motive of Klaus (1963a) to separate the genera. However, the idea of "page priority" is not provided by the International Code of Botanical Nomenclature. Art. 51 is very plain when it states:

" . . . The author who first unites taxa bearing names or epithets of the same date *has the right to choose one of them*, and his choice must be followed".

Bharadwaj did not make use of "the right to choose one of them", but yet "his choice must be followed".

Lunatisporites is restricted to forms without a monolete or reduced trilete mark in the proximal intexine of the central body. As for the existence of these characteristics we refer to the description of *Taeniaepollenites* n. gen. (remarks, p. 360). *Lunatisporites* differs from *Protohaploxypinus* Samoilovich 1953 emend. Hart 1964 and *Striatopodocarpites* Sedova 1956 emend. Bharadwaj 1962 by the presence of a biconvex germinal area and narrow equatorial bladder connections.

Lunatisporites puntii n. sp.

Fig. 25; Plate XIV, Figs. 1, 2, 3, 4.

Holotype: *Lunatisporites puntii* n. sp. Single grain slide 31-HV-239; Plate XIV, Fig. 3.

Derivatio nominis: Dr W. Punt, Pollenmorphological Laboratories of the Botanical Museum and Herbarium of the State University, Utrecht, the Netherlands.

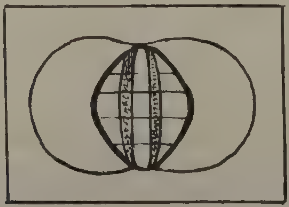


Fig. 25. *Lunatisporites puntii*

Diagnosis: Pollen bisaccate, striate. Equator of central body approx. circular to transversely elliptical or subangular (rhombic). Thickened proximal exoexine with 4–6 taeniae in polar view, frequently of unequal width, usually separated by very narrow sutures. Taeniae with fine infrastructure. Proximal intexine without tetrad mark. Sacci more or less diploxylonoid to platysaccoid, distally inclined, laterally very close to each other or even equatorially interconnected. Sacci very finely infrareticulate. Distal germinal area in principle biconvex, frequently accompanied by transversal compression folds. Known size range 79–119 μ (holotype 115 μ).

Remarks and comparisons: Within the variation of the species the shape of the sacci is liable to rather important divergences. Specimens with sutures between the taeniae – a characteristic of *Taeniaepollenites* n. gen. – are uncommon. A few specimens with remarkably deformed taeniae have been found (Plate XIV, Fig. 4). *L. puntii* differs from *Lunatisporites acutus* Leschik 1956a especially by its bigger size.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).
Occurrence: Röt salinar of Hengelo; rare.

Striatoabietites Sedova 1956 emend. Hart 1964

Type species: *Striatoabietites bricki* Sedova 1964, t. 41, f. 5.

Comparison: Striatoabietites differs from *Tubantiapollenites* n. gen. by the absence of a reduced trilete (roof-shaped) or monolete (straight) mark in the proximal intexine.

Striatoabietites aytugii n. sp.
Fig. 26; Plate XVII, Figs. 3, 4, 5, 6.

Holotype: *Striatoabietites aytugii* n. sp. Single grain slide 31-HV-114; Plate XVII, Fig. 3.
Derivatio nominis: B. Aytug, Faculty of Forestry, University of Istanbul, Turkey.

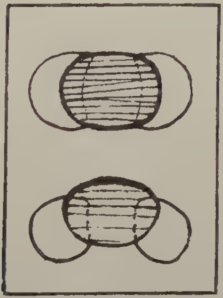


Fig. 26. *Striatoabietites aytugii*

Diagnosis: Pollen bisaccate, multistriate. Equator of central body strongly longitudinally elliptical. Thickened proximal exoexine with 10–14 taeniae in polar view; taeniae finely infragranulate, separated by very narrow sutures. Proximal intexine without (reduced) trilete or monolete mark. Sacci more or less diploxylonoid, distally inclined, finely infrareticulate. Very wide distal germinal area. Known size range 60–80 μ (holotype 75 μ).

Remarks and comparisons: Usually the shape is faintly diploxylonoid but occasionally it may become more pronounced. *S. aytugii* differs from *Tubantiapollenites balmei* (Klaus 1964) nov. comb. by the absence of a (reduced) trilete or monolete mark in the proximal intexine.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 392 m (Röt salinar).
Occurrence: Regularly recognized in the Hengelo Röt salinar; never in high percentages.

SUBINFRATURMA *Triletestriatiti* nov. subinfraturma.

Diagnosis: Pollen bisaccate, striate. Intexine of the central body with a proximal trilete, reduced trilete (roof-shaped) or monolete mark.

Remarks: See *Aletestriatiti* nov. subinfraturma (remarks, p. 353).

Taeniaepollenites n. gen.

Type species: *Taeniaepollenites jonkeri* n. sp., Plate XVIII, Figs. 1A, B, C.

Diagnosis: See diagnosis of *Taeniaesporites* Leschik 1956a emend. KLAUS 1963a (KLAUS 1963a, pp. 306–307). This excellent diagnosis can serve without restrictions as a description of a new striate genus, which includes among others all the forms recognized by KLAUS (1963a).

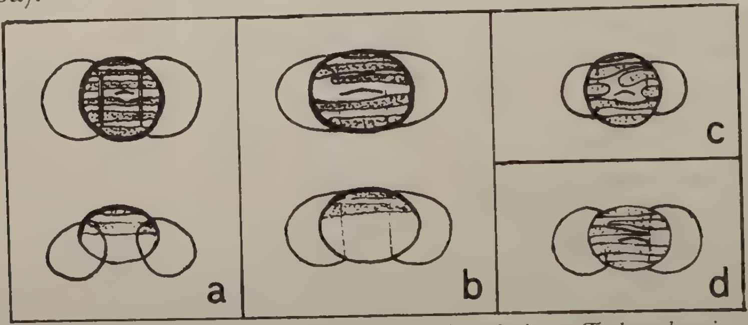


Fig. 27. *Taeniaepollenites*. a. *T. multiplex;* b. *T. jonkeri;* c. *T. hengeloensis;* d. *T. discrepans*

Remarks and comparisons: We consider the presence or absence of a (reduced) trilete or monorete mark in the proximal intexine of striate pollen a very important feature. With the exception of KLAUS (1963a) little attention has been paid to this characteristic.

Since species of *Taeniaepollenites* n. gen. were mostly placed within the genus *Taeniaesporites* Leschik 1956a and since the latter genus has to be considered a synonym of *Lunatisporites* Leschik 1956a emend Bharadwaj 1962 (compare p. 357), it seems useful to check the concepts about the intexinal Y-mark within these genera.

LESCHIK (1956a) creates both *Lunatisporites* and *Taeniaesporites*, not mentioning the existence of an Y-mark. Also the illustrations do not show a tetrad mark. However, the genera are placed within the *Disacciatriletes*.

LESCHIK (1956b) also describes *Taeniaesporites noviaulensis* from the German Zechstein deposits. A monolete mark is clearly visible and is mentioned in the description.

GREBE (1957) considers both *Lunatisporites* and *Taeniaesporites* synonyms of *Lueckisporites* Potonié & Klaus 1954 (*Lueckisporites* was considered to include "bisaccate spores without Y-mark", even after the emendation by POTONIÉ 1958; JANSONIUS 1962 states that "a monolete mark may be present"; only KLAUS 1963a recognizes the fundamentally trilete character). *T. noviaulensis* should be identical with *Lueckisporites virkkiae* Potonié & Klaus 1954.

In principle POTONIÉ (1958) follows GREBE (1957); however, he maintains the species "*Lueckisporites*" *noviaulensis*; nothing is to be said about the monolete mark. *Lunatisporites* remains separate; like Grebe, Potonié has restudied the type species but an Y-mark was not demonstrated. Various authors (e.g. LAKHANPAL, SAH and DUBE 1960; POTONIÉ and LELE 1961) continued to interpret *Lunatisporites* in this way.

LESCHIK (1959) points out the differences between his alete Triassic species and his Permian *T. noviaulensis*. KLAUS (1960) follows GREBE (1957); he finds "*Lueckisporites kraeuseli*" in Keuper sediments; pollen without Y-mark.

BHARADWAJ (1962) considers *Taeniaesporites* a synonym of *Lunatisporites* Leschik 1956a emend. Bharadwaj 1962, which does not possess a tetrad mark. In India this concept is commonly followed. We agree with it too (compare p. 357).

JANSONIUS (1962) emends the generic diagnosis of *Taeniaesporites* and also describes some new species. Nothing is stated about a possible tetrad mark. There is a strong resemblance with European monolete species. Particularly *Taeniaesporites novimundi* Jansonius 1962 reminds us of *T. noviaulensis*. However, studying some of Jansonius' slides we have not been able to recognize a convincing tetrad mark within the Canadian species. Yet they differ from *Lunatisporites* Leschik 1956a emend. Bharadwaj 1962.

ORŁOWSKA ZWOLIŃSKA (1962) determines *T. noviaulensis* from the Polish Upper Permian deposits; she mentions the monolete mark.

GREBE and SCHWEITZER (1962) do not pay attention to the monolete mark of *Lueckisporites noviaulensis* (Leschik 1956a) Potonié 1958.

BALME (1963) follows JANSONIUS (1962) but he mentions the monolete marks both of cf. *T. noviaulensis* and *Taeniaesporites obex* Balme 1963. In his illustrations the marks are well visible.

SCHAARSCHMIDT (1963a) considers *Taeniaesporites* a synonym of *Striatites* Pant 1955. Some species, like *Striatites noviaulensis* (Leschik 1956a) Schaarschmidt 1693, may possess a proximal monolete mark.

By emending *Taeniaesporites*, KLAUS (1963a) gives an excellent diagnosis for the monolete forms. In fact all his new species are monolete. So they must be compared with *T. noviaulensis* instead of with *T. kraeuseli*, the type species of the genus.

A clear intexine-mark is also visible in the illustrations of *T. noviaulensis* from the Zechstein of Thüringen (ULLRICH 1964).

In his generic descriptions of striate pollen HART (1964) does not reckon with possible tetrad marks. With regard to *Taeniaesporites* he follows Jansonius' emendation. He considers the mark of *T. obex* a species-characteristic, suppressing it, however, when describing *T. noviaulensis* (syn: *T. novimundi*).

Bharadwaj and Singh (1964) also recognize *Lunatisporites acutus* Leschik 1956a in the Austrian Upper Triassic. They do not mention the presence of a tetrad mark. Within European Bunter and Muschelkalk sediments Klaus (1964) recognizes *T. novimundi*. Not mentioning the tetrad mark, he classes this species together with the monolete *Taeniaesporites austriacus* Klaus 1964, under the *Disaccimonoletes* Klaus 1963a. This infraturma is considered to contain bisaccate monolete pollen but, however, it excludes striate pollen.

In Freudenthal's (1964) opinion the specimens from the Dutch Bunter belong to *T. noviaulensis* (syn: *T. novimundi*). The tetrad mark is visible in his illustrations but it is not drawn into the discussion. Also Schulz (1964) compares his specimen from the Middle Bunter with *noviaulensis*; nothing is stated about a possible monolete mark.

According to this enumeration it is clear that there is no unanimity about the importance of the presence or absence of a monolete tetrad mark. This should be regarded a grave hiatus, particularly because within the Hengelo assemblage we recognize both forms habitu *Lunatisporites* Leschik 1956a emend Bharadwaj 1962, without a tetrad mark, and forms habitu *Taeniaesporites* Leschik 1956a emend. Klaus 1963a with well-developed monolete or reduced trilete marks. So we want to separate them strictly.

The genus *Taeniaesporites* cannot be maintained because it is a synonym of *Lunatisporites* (compare p. 358; also in the case of separating these genera one has to realize that the type species of *Taeniaesporites* does not possess a tetrad mark). So the genus *Taeniaepollenites* n. gen. is proposed, including species with monolete or reduced trilete marks. Choosing this related name may cause confusion, but we want to keep the prefix *Taeniae-*.

Taeniaepollenites n. gen. can be distinguished from *Lueckisporites* Potonié & Klaus 1954 emend. Klaus 1963a by possessing more taeniae. The taeniae of *Strotersporites* Wilson 1962 emend. Klaus 1963a are not differentiated into polar and equatorial taeniae. *Lunatisporites* Leschik 1956a emend. Bharadwaj 1962 is alete and has a narrow biconvex germinal area; furthermore its saccus infrareticulum is very fine, the sacci are very close to each other or even equatorially interconnected and the equator of the central body is usually transversely elliptical.

Taeniaepollenites jonkeri n. sp.

Fig. 27b; Plate XVIII, Figs. 1A, B, C, 2; Plate XIX, Fig. 1.

Holotype: *Taeniaepollenites jonkeri* n. sp. Single grain slide 31-HV-209; Plate XVIII, Figs. 1A, B, C.

Derivatio nominis: Prof. Dr. F. P. Jonker, Botanical Museum and Herbarium of the State University, Utrecht, the Netherlands.

Diagnosis: Pollen bisaccate, striate. Equator of the central body longitudinally elliptical. Thickened proximal exoexine differentiated into 2 equatorial taeniae and 2–4 polar taeniae. The taeniae are separated by rather wide sutures; they are pronounced infragranulate, frequently the margins are more or less crenulate. Proximal intexine with reduced trilete to monolete mark. Sacci haploxylonoid, hardly distally inclined; meshes of saccus-infrareticulum 1–2.5 μ wide. Wide distal germinal area with approx. structureless exine. Known size range 75–110 μ (holotype 95 μ).

Remarks and comparisons: In principle there are 2 polar taeniae but these can be divided. Specimens with 3 or 4 polar taeniae are very frequent and even specimens with 2½ or 3½ taeniae are common.

T. jonkeri differs from *Taeniaepollenites multiplex* n. sp. and *Taeniaepollenites discrepans* n. sp. by its haploxylonoid shape. *Taeniaepollenites hengeloensis* n. sp. possesses reduced sacci. These newly described species differ from the *Taeniaepollenites*-species from European Upper Permian assemblages (≡ "*Taeniaesporites*" *with* proximal intexine-mark; compare p. 360) by their relatively finer saccus-infrareticulum.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).

Occurrence: Regularly recognized in the Hengelo Röt salinar; never in high percentages.

Taeniaepollenites multiplex n. sp.

Fig 27a; Plate XIX, Figs. 6, 7.

Holotype: *Taeniaepollenites multiplex* n. sp. Single grain slide 31-HV-39; Plates XIX, Fig. 6.

Diagnosis: Pollen bisaccate, striate. Equator of the central body approx. circular to longitudinally elliptical. Thickened proximal exoexine, differentiated into 2 equatorial taeniae and 2–4 polar taeniae. The taeniae are separated by rather wide sutures; they are pronounced infragranulate, frequently the margins are more or less crenulate. Proximal intexine with reduced trilete to monolete mark. Sacci faintly to strongly diploxylonoid, strongly distally inclined; meshes of saccus-infrareticulum 1–3 μ wide. Wide distal germinal area with approx. structureless exine. Known size range 80–105 μ (holotype 84 μ).

Remarks and comparisons: Specimens with 2, 2½, 3, 3½, and 4 polar taeniae were recognized (compare *T. jonkeri*, remarks above). The appearance of an elliptical equator is mostly attended with a more pronounced diploxylonoid shape. There are, however, progressive transitions to faintly diploxylonoid forms with a circular equator. So a separation seems undesirable.

T. multiplex differs from *Taeniaepollenites discrepans* n. sp. by its thickened proximal exoexine with pronounced infragranulate taeniae. The species differs from *Taeniaepollenites jonkeri* n. sp. and *Taeniaepollenites hengeloensis* n. sp. by its diploxylonoid shape.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).

Occurrence: Most common striate species in the Hengelo Röt salinar but never reaching high percentages. Also recognized in the overlying Röt pelites.

Taeniaepollenites discrepans n. sp.

Fig. 27d; Plate XVIII, Fig. 3.

Holotype: *Taeniaepollenites discrepans* n. sp. Single grain slide 31-HV-125; Plate XVIII, Fig. 3.

Diagnosis: Pollen bisaccate, striate. Equator of the central body approx. circular to longitudinally elliptical. Hardly thickened proximal exoexine differentiated into 2 equatorial taeniae and 2–5 polar taeniae. The taeniae are separated by rather wide sutures; they are faintly infrastructured. Proximal intexine with reduced trilete to monolete mark. Sacci diploxylonoid, distally inclined; meshes of saccus-infrareticulum 1–2 μ wide. Wide distal germinal area with approx. structureless exine. Known size range 90–100 μ (holotype 98 μ).

Remarks and comparisons: In principle there are 2 polar taeniae; they can be split up into more exoexinal strips, which are sometimes incompletely developed (compare *T. jonkeri*, remarks p. 363). *T. discrepans* differs from *Taeniaepollenites multiplex* n. sp. by its hardly thickened proximal exoexine without pronounced infragranulate structure. *Taeniaepollenites jonkeri* n. sp. and *Taeniaepollenites hengeloensis* n. sp. are haploxylonoid and possess also a thickened proximal exoexine.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 392 m (Röt salinar).
Occurrence: Röt salinar of Hengelo; rare.

Taeniaepollenites hengeloensis n.sp.

Fig. 27c; Plate XIX, Fig. 2.

Holotype: *Taeniaepollenites hengeloensis* n. sp. Single grain slide 31-HV-16; Plate XIX, Fig. 2.
Derivatio nominis: named for the city of Hengelo, the Netherlands.

Diagnosis: Pollen bisaccate, striate. Equator of the central body approx. circular. Thickened proximal exoexine differentiated into 2 equatorial taeniae and 2–4 polar taeniae. The taeniae are separated by rather wide sutures; they are pronounced infragranulate, frequently the margins are more or less crenulate. Proximal intexine with reduced trilete to monolete mark. Sacci haploxylonoid, strongly reduced; meshes of saccusinfrareticulum 1–2.5 μ wide. Wide distal germinal area with approx. structureless exine. Known size range 80–90 μ (holotype 84 μ).

Remarks and comparisons: In principle there are 2 polar taeniae; they can be split up into more exoexinal strips which are sometimes incompletely developed (compare *T. jonkeri*, remarks, p. 363). *T. hengeloensis* differs from *Taeniaepollenites jonkeri* n. sp. by its reduced sacci and the circular equator. *Taeniaepollenites multiplex* n. sp. and *Taeniaepollenites discrepans* n. sp. are diploxylonoid.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 404 m (Röt salinar).
Occurrence: Röt salinar of Hengelo; very rare.

Tubantiapollenites n. gen.

Type species: *Tubantiapollenites striatitoides* n. sp., Plate XIX, Fig. 3.
Derivatio nominis: Tubantia, Latin name for Twente, the region from which our samples originate.

Diagnosis: Pollen bisaccate, multistriate. Slightly thickened proximal exoexine differentiated into a great number of taeniae; these are separated by very narrow sutures. Proximal intexine with reduced trilete (roof-shaped) to monolete (straight) mark. Sacci haploxylonoid or faintly diploxylonoid. Wide distal germinal area.

Remarks and comparisons: Except *Striatoabietites balmei* Klaus 1964

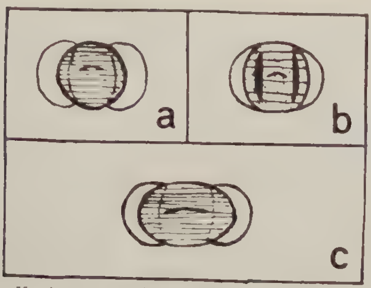


Fig. 28. *Tubantiapollenites*. a. *T. schulzii*; b. *T. striatitoides*; c. *T. balmei*

we did not find in the palynological literature multistriate species built up according to the description of *Tubantiapollenites* n. gen. We consider the presence or absence of an intexinal tetrad mark a very important feature and we want to separate the monolete or trilete species strictly from genera like *Striatites* Pant 1955 emend. Klaus 1963a, *Striatoabietites* Sedova 1956 emend. Hart 1964, etc. The Y-mark is not always clearly visible; before claiming multistriate species alete it is advisible to study sufficient specimens. *Strotersporites* Wilson 1962 emend. Klaus 1963a differs by possessing a wide rupture between the medial taeniae. *Taeniaepollenites* n. gen. is distinguished by a differentiation into polar and equatorial taeniae.

Tubantiapollenites striatitoides n. sp.

Fig. 28b; Plate XIX, Fig. 3.

Holotype: *Tubantiapollenites striatitoides* n. sp. Single grain slide 31-HV-40; Plate XIX, Fig. 3.

Derivatio nominis: Apart from the tetrad mark, the new species reminds one of *Striatites* Pant 1955 emend. Klaus 1963a.

Diagnosis: Pollen bisaccate, multistriate. Equator of the central body approx. circular to subangular. Slightly thickened proximal exoexine differentiated into taeniae (7–10 visible in polar view); taeniae finely infragranulate, separated by very narrow sutures. Proximal intexine with reduced trilete to monolete mark. Small sacci, haploxylonoid, semi-lunar, finely infrareticulate. Wide distal germinal area, usually limited by compression folds. Known size range 60–65 μ (holotype 64 μ).

Remarks and comparisons: Often specimens of *T. striatitoides* tend to release the sacci. The species differs from *Tubantiapollenites schulzii* n. sp. by the small haploxylonoid sacci. *Tubantiapollenites balmei* (Klaus 1964) nov. comb. possesses a longitudinally elliptical equator. Furthermore, compared with the two other species, *T. striatitoides* possesses a smaller number of taeniae.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).
Occurrence: Röt salinar of Hengelo; rare.

Tubantiapollenites balmei (Klaus 1964) nov. comb.

Fig. 28c; Plate XIX, Fig. 5.

Holotype: *Tubantiapollenites* (al. *Striatoabietites*) *balmei* (Klaus 1964) nov. comb.; Klaus 1964, t. 2, f. 17.

Remarks and comparisons: On account of the presence of a proximal intexine-mark Klaus' species is considered as *Tubantiapollenites* n. gen. The length of the roof-shaped or straight mark is rather variable; forms with elongated marks predominate, but there is no reason to propose a separation.

In polar view 13–20 taeniae are visible. Observed size range 40–70 μ. The longitudinally elliptical equator of the central body is characteristic; by this feature *T. balmei* can be distinguished from *Tubantiapollenites schulzii* n. sp. and *Tubantiapollenites striatitoides* n. sp.; Moreover, the latter species is haploxylonoid.

Occurrence: Röt salinar of Hengelo; rare. Klaus (1964) mentions *T. balmei* from German, French and Italian Muschelkalk assemblages.

Tubantiapollenites schulzii n. sp.

Fig 28a; Plate XIX, Fig 4.

Holotype: *Tubantiapollenites schulzii* n. sp. Single grain slide 31-HV-113; Plate XIX, Fig. 4.

Derivatio nominis: Dr E. Schulz, Zentrales Geologisches Institut, Berlin, Germany.

Diagnosis: Pollen bisaccate, multistriate. Equator of central body approx. circular. Slightly thickened proximal exoexine differentiated into taeniae (10–15 μ visible in polar view); taeniae finely infragranulate, separated by very narrow sutures. Proximal intexine with reduced trilete or monolete mark. Sacci diploxylonoid, finely infrareticulate. Wide distal germinal area. Known size range 46–56 μ (holotype 51 μ).

Remarks and comparisons: Often the intexinal mark of *T. schulzii* is hardly visible. *Protosacculina jansonii* Freudenthal 1964 may be considered conspecific with this species; we restudied the holotype but could not demonstrate the intexinal mark with certainty. To propose a new combination seems incorrect, because in that case "*Tubantiapollenites jansonii*" should be based on a holotype without the characteristic tetrad mark. *T. schulzii* differs from *Tubantiapollenites balmei* (Klaus 1964) nov. comb. by its circular equator. *Tubantiapollenites striatitoides* n. sp. possesses small haploxylonoid sacci and a smaller number of taeniae.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 392 (Röt salinar).
Occurrence: Röt salinar of Hengelo; rare.

Turma *Monocolpates* (Wodehouse 1935) Iversen and Troels-Smith 1950
Subturma *Intorti* (Naumova 1937) Potonié 1958

Cycadopites (Wodehouse 1933) ex Wilson & Webster 1946

Type species: *Cycadopites fellicularis* Wilson & Webster 1946, p. 274, f. 7.

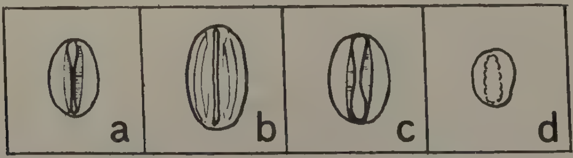


Fig. 29. *Cycadopites*. a. *C. coxii*; b. *C. trusheimii*; c. *C. sufflavus*; d. *C. crenulatus*

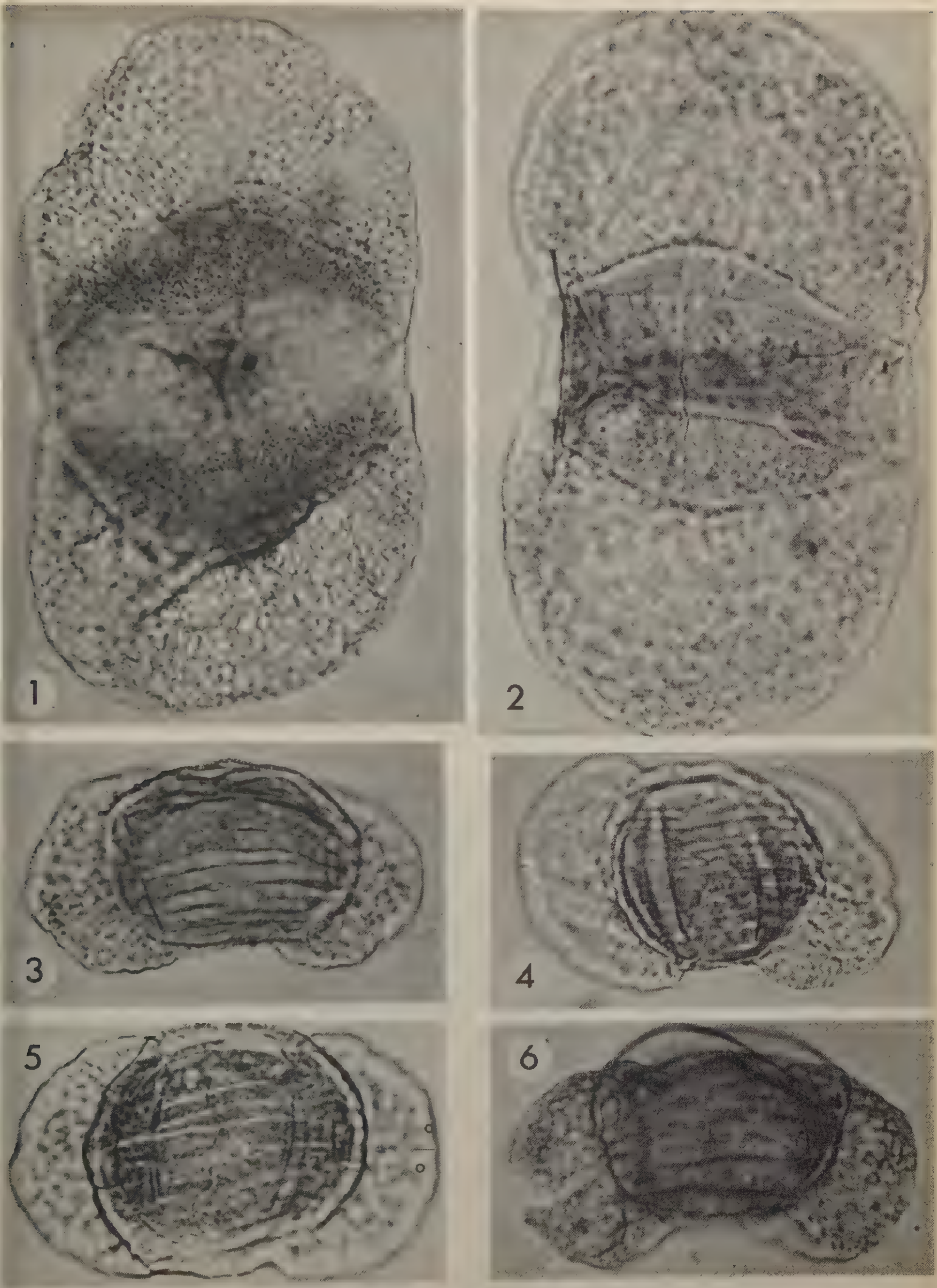


Plate XVII. 1. *Angustisulcites grandis*; 2. id.; 3. *Striatoabietites aytugii*, holotype; 4. id.; 5. id.; 6. id., equatorial view. (all specimens 750 ×).

PLATE XVII

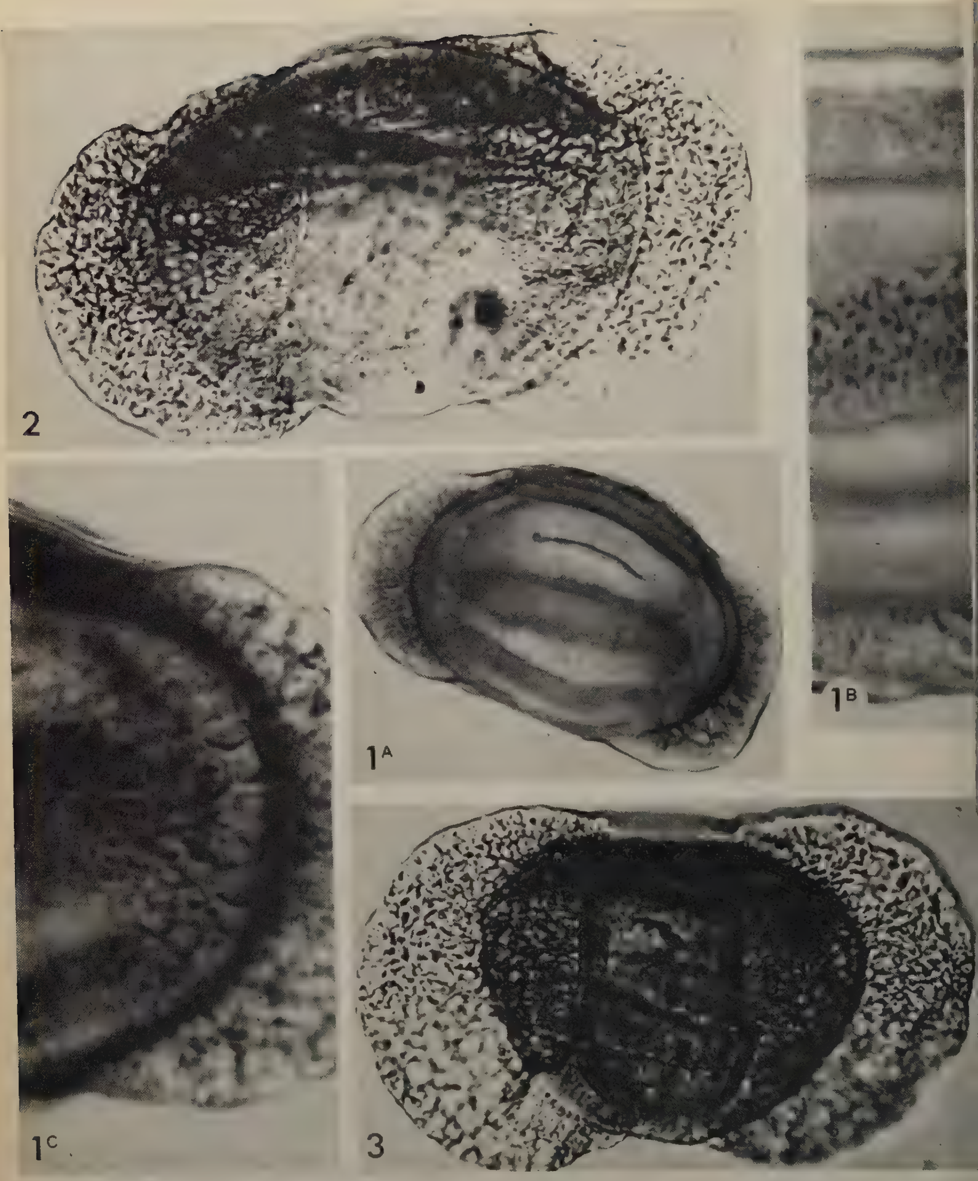


Plate XVIII. 1A. *Taeniaepollenites jonkeri*, holotype (700 ×); 1B, 1C. details, showing structure; 2. id., equatorial view (875 ×); 3. *Taeniaepollenites discrepans*, holotype (850 ×).

PLATE XVIII

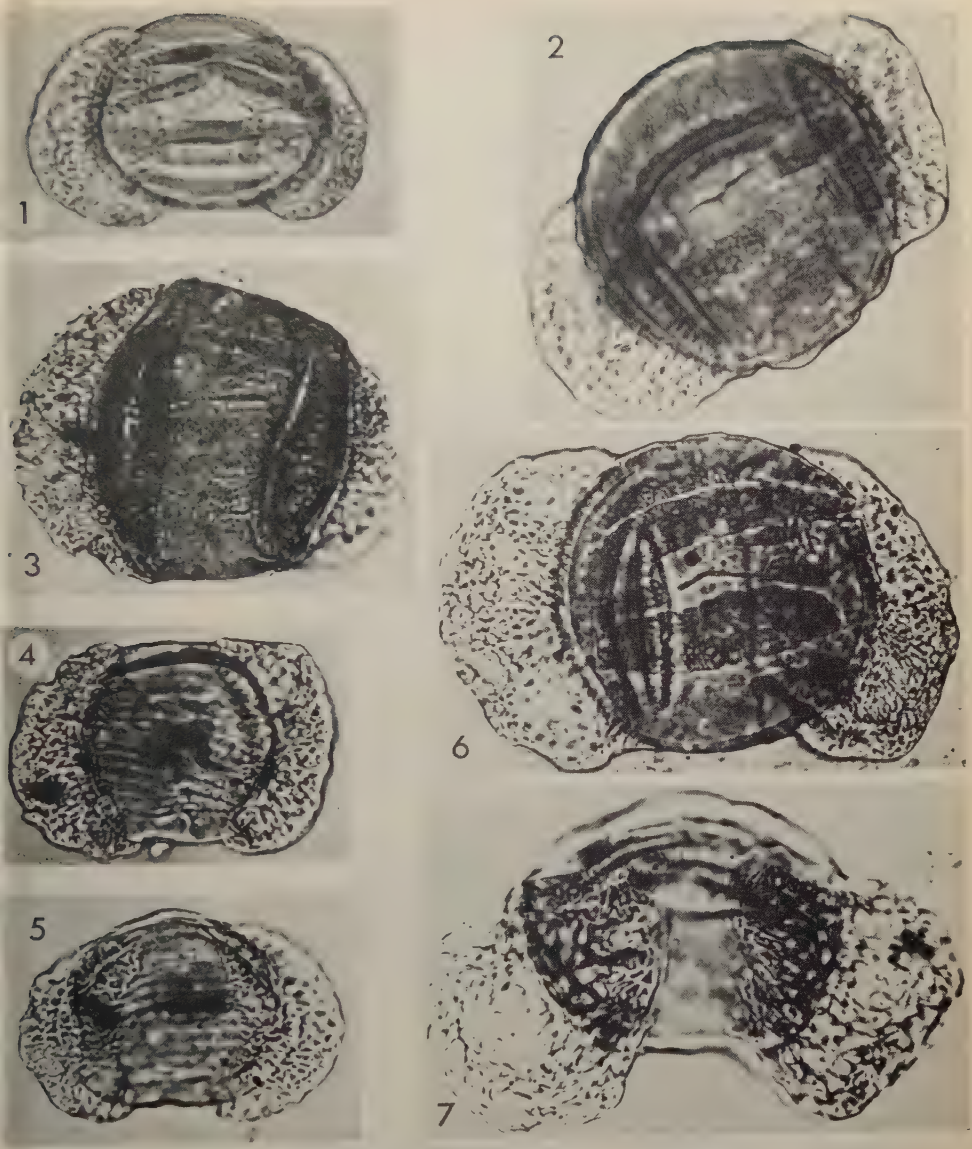


Plate XIX. 1. *Taeniaepollenites jonkeri* (500 ×); 2. *Taeniaepollenites hengeloensis*, holotype (700 ×); 3. *Tubantiapollenites striatitoides*, holotype (850 ×); 4. *Tubantiapollenites schulzii*, holotype (850 ×); 5. *Tubantiapollenites balmei* (850 ×); 6. *Taeniaepollenites multiplex*, holotype (700 ×); 7. id., equatorial view (700 ×).

PLATE XIX

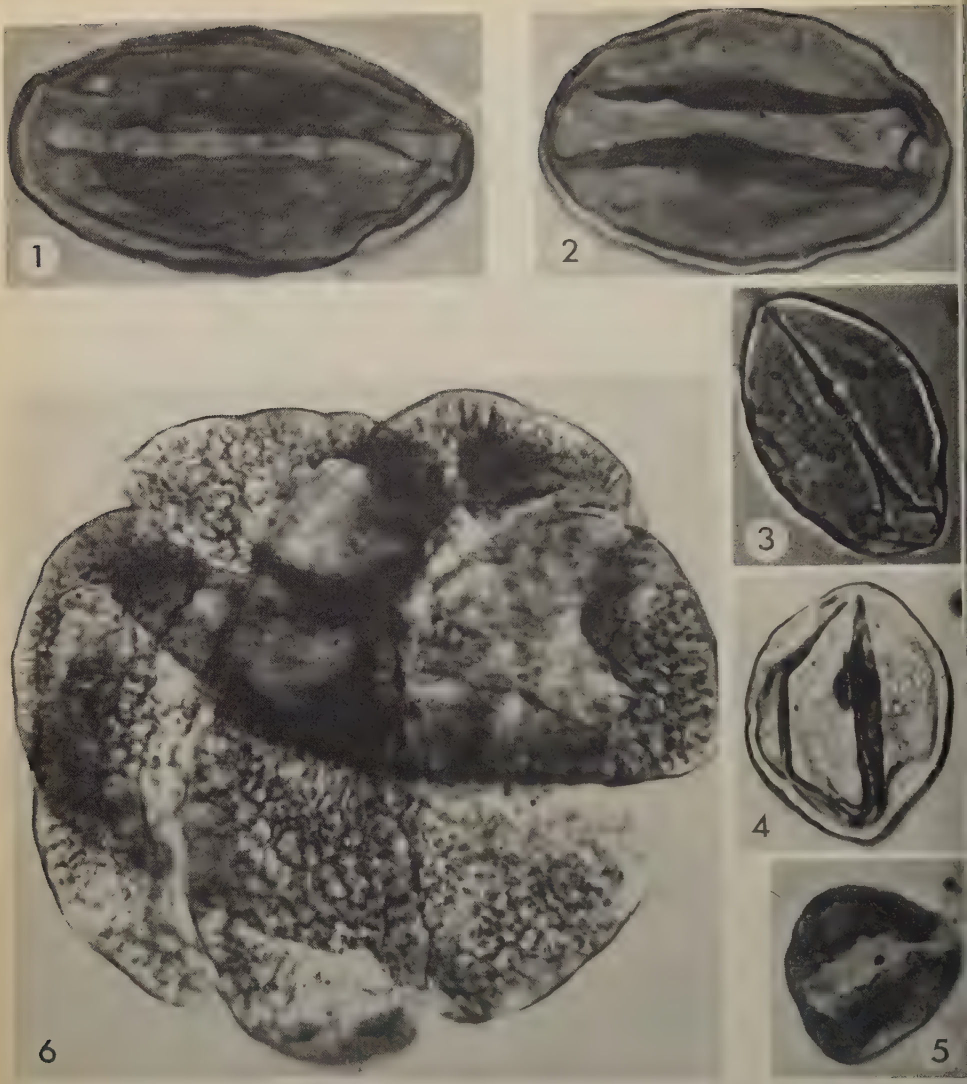


Plate XX. 1. *Cycadopites trusheimii*, holotype; 2. *Cycadopites sufflavus*, holotype; 3. *Cycadopites coxii*, holotype; 4. id.; 5. *Cycadopites crenulatus*, holotype; 6. Incert. sed. (all specimens 1200 ×).

PLATE XX

Remarks and comparisons: A generic differentiation of monocolpate pollen grains is hampered by the few characteristics which can be used in describing the species; this is due to the relatively simple shape. So provisionally it seems more reasonable to use the genus *Cycadopites* in a very broad sense (compare e.g. JANSONIUS 1962). Even the relation with *Monosulcites* (Cookson 1947) ex Couper 1953 is not clear; within the variation of a species both *Cycadopites*-like specimens and forms corresponding to the description of *Monosulcites* are found.

Cycadopites coxii n. sp.

Fig 29a; Plate XX, Figs 3, 4

Holotype: *Cycadopites coxii* n. sp. Single grain slide 31-HV-259; Plate XX, Fig. 3.

Derivatio nominis: R. Cox, Koninklijke Nederlandsche Zoutindustrie, Hengelo, the Netherlands.

Diagnosis: Pollen monocolpate with approx. elliptical outline. Thin exine with fine infrastructure. Sulcus lemniscatoid to irregularly elliptical depending on the fossilisation. Size very constant (28–31 μ).

Remarks and comparisons: Many specimens show a wide sulcus, which is not lemniscatoid; these forms should have been considered as *Monosulcites* Cookson 1947 ex Couper 1953. However, they can be derived from true lemniscatoid *Cycadopites* forms by progressive transitions.

C. coxii differs from *Cycadopites sufflavus* n. sp. by its smaller size; the size range of the latter species is also very constant (42–45 μ); transitions were not recognized, so a separation of the species seems justified.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).

Occurrence: Regularly recognized in the Röt salinar of Hengelo; low percentages.

Cycadopites sufflavus n. sp.

Fig 29c; Plate XX, Fig. 2.

Holotype: *Cycadopites sufflavus* n. sp. Single grain slide 31-HV-90; Plate XX, Fig. 2.

Diagnosis: Pollen monocolpate with approx. elliptical outline. Thin exine with fine infrastructure. In principle the sulcus possesses a lemniscatoid shape, but elongated elliptical outlines appear frequently. Size very constant (42–45 μ).

Remarks and comparisons: Within the variation of *C. sufflavus* occur *Monosulcites*-like forms (compare *C. coxii*; remarks p. 367). *C. sufflavus* is very related to *Cycadopites coxii* n. sp., but the absence of transitional sizes justifies a separation. *Cycadopites trusheimii* n. sp. differs by its bigger size and its characteristic folding.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 392 m (Röt salinar).

Occurrence: Regularly recognized in the Röt salinar of Hengelo; low percentages.

Cycadopites trusheimii n. sp.

Fig 29b; Plate XX, Fig. 1.

Holotype: *Cycadopites trusheimii* n. sp. Single grain slide 31-HV-260; Plate XX, Fig. 1.

Derivatio nominis: Dr. F. Trusheim, Gewerkschaft Brigitta, Hannover, Germany.

Diagnosis: Pollen monocolpate with approx. elliptical outline. Thin exine with fine infrastructure. Sulcus usually lemniscatoid to elongated elliptical. Parallel to sulcus a varying number of narrow folds. Size very constant (54–58 μ).

Remarks and comparisons: We consider the presence of the narrow folds an important characteristic; within the variation of *Cycadopites coxii* n. sp. and *Cycadopites sufflavus* n. sp. this type of folding never appears.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 405.50 m (Röt salinar).

Occurrence: Röt salinar of Hengelo; rare.

Cycadopites crenulatus n. sp.

Fig. 29d; Plate XX, Fig. 5.

Holotype: *Cycadopites crenulatus* n. sp. Single grain slide 31-HV-79; Plate XX, Fig. 5.

Diagnosis: Pollen monocolpate with irregular elliptical outline. Thin exine with rather pronounced infragranulate structure. Wide sulcus with crenulate margin. Small sizes, very constant (18–21 μ).

Remarks and comparisons: A lemniscatoid sulcus has never been recognized; so the species might belong to *Monosulcites* Cookson 1947 ex Couper 1953. However, the relations between *Cycadopites* and *Monosulcites* are not very clear to us (p. 367). It seems therefore preferable to consider the species as *Cycadopites*. It differs from *Cycadopites coxii* n. sp., *Cycadopites sufflavus* n. sp. and *Cycadopites trusheimii* n. sp. by its very small size, its crenulate sulcus margin and a more pronounced infrastructure.

Locus typicus: Boring 31, K.N.Z., Hengelo; depth 411.50 m (Röt salinar).

Occurrence: Regularly recognized in the Röt salinar of Hengelo; low percentages.

Incertae sedis

A few specimens of rather particular plant microfossils were found in the palynological assemblage of Hengelo (Plate XX, Fig. 6). These bodies consist of some twisted strips of a material remarkably resembling the infrareticulate saccus exine of saccate pollen. Size approx. 80 μ.

ACKNOWLEDGEMENTS

The author wishes to express his sincere appreciation to Professor Dr. F. P. Jonker for proposing and stimulating this investigation and to Dr. W. Punt for his guidance in the delicate fields of pollenmorphology and botanical nomenclature and taxonomy.

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Thanks are especially due to the Koninklijke Nederlandsche Zoutindustrie for supplying the requisite rock samples.

APPENDIX

Some important papers on Permian and Triassic palynology became available to us after finishing the present investigation [1]).

We regret the fact of being unable to make use of the information derived from them. Apart from some inevitable synonyms these papers give further information about the horizontal and vertical distribution of Lower Mesophytic pollen and spores in Europe.

Mädler (1964) has described palynological assemblages from the Röt, Lower Muschelkalk and Keuper of Germany. Other data from the Röt is given by Schulz (1965) and by Reinhardt and Schmitz (1965). An important stratigraphic diagram is published by Klaus (1965). Finally, I ought to mention two papers by Clarke (1965a, b) on Keuper and Permian palynology, respectively.

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[1]) Clarke, R. F. A. 1965a. Keuper miospores from Worcestershire, England. Palaeontology **8**: 294–321.
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POLLEN-ANALYTICAL INVESTIGATIONS IN THE COASTAL DUNE AREA NEAR THE HAGUE, THE NETHERLANDS

J. H. A. BOERBOOM AND W. H. ZAGWIJN

(*State Agricultural University, Wageningen, and Geological Survey, Haarlem*)

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ABSTRACT

This paper deals with the results of field reconnaissance and pollen-analysis of peatbeds occurring in the Dune area near the city of The Hague (The Netherlands). Such peatbeds were known already to occur at the surface as filling of depressions (former beach plains) of the Older Dune system, outside the area covered by Younger Dunes. It could be shown that below the latter a very similar pattern of peat-filled depressions exists.

Pollen-analysis and radiocarbon dating indicate that formation of Old Dune sand took place until about the beginning of our era, though it might in places have been interrupted by a forest-phase at the end of Subboreal times, around 1200 B.C. In part vegetation was characterised by dune-shrub, including not only *Hippophaë* but also commonly *Juniperus*. After the formation of the Older Dunes a period of reafforestation followed, which in the western-most coastal area came to an end by the formation of the Younger Dunes, which event in this area could be dated around 1000–1200 A.D.

1. INTRODUCTION

Though pollen-analytical investigations of Holocene beds have been published from many parts of the Netherlands, the coastal dune area has been neglected so far. This paper is a first attempt to fill at least part of this gap in our knowledge.

It is a well-known feature that in many places along the coast of the western Netherlands two dune systems of Holocene age can be recognized, called Older and Younger Dunes (JESWIET, 1913; VAN BAREN, 1913; TESCH 1920–30). The Older Dunes occur as low NE-SW ridges, and were formed on top of an ancient coastal barrier system. Between these ridges peat-filled depressions occur. The Younger Dunes show much more relief (VANHOUTEN, 1939; BOERBOOM, 1957), revealing more or less distinct systems of parabolae and often attaining a height of 20–40 m.

In the vicinity of The Hague the two dune systems are well represented; the Older Dunes occur at the surface in the eastern part of the area, whereas in the western part they are overlain by Younger Dunes (Fig. 1).

Part of the Younger Dune area is utilized as catchment area for the Dune Water Works of The Hague. Artificial infiltration of river water into the dune-pans is now applied on a large scale, for which preliminary studies had to be made. A map has been compiled showing the occurrence of peatbeds in this area. About 1200 shallow borings

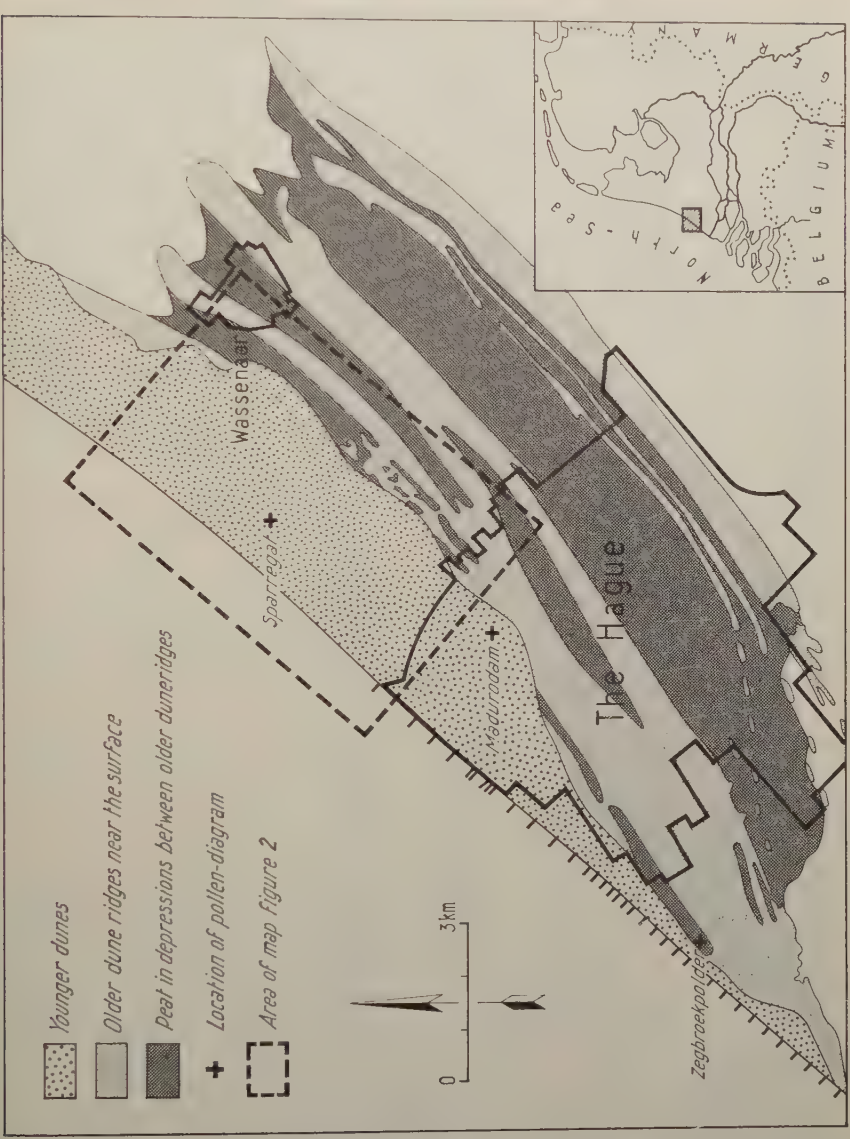

Fig. 1. Map showing pattern of Older and Younger Dunes near The Hague Location of pollen-diagrams (Sources: Geological Map; Haans and Maarleveld 1965; unpubl. data).

were made for this purpose in this area of 1800 ha. As the peatbedt were shown to occur between about 1 m above to 2 m below presens sealevel, and the present surface of the dune-pans is at about 4–7 m above sealevel, it was sufficient to bore 3–9 m deep.

The map compiled by the Dune Water Works in 1956 showing the peatbeds has served as a basis for Fig. 2.

Three pollen-diagrams, prepared by the second author and giving some insight into history of the dune-vegetation near The Hague, will also be discussed in this paper. One is derived from peatbeds found in a boring in the water catchment area (Meyendel–Sparregat Fig. 4, location Figs. 1, 2), at a spot where two peatbeds occurred (Fig. 2). The lower peatbed of 40 cm consisted of sedge peat containing a fair amount of windblown sand overlain by reed peat, which points to somewhat wetter conditions. The upper peatbed of 18 cm showed a normal succession of reed peat below, overlain by sandy sedge peat. Between the two beds nearly 50 cm of dune-sand was found (Fig. 4).

The two other diagrams come from peatbeds found in borings outside this area (Madurodam Fig. 5 and Zegbroekpolder Fig. 6, location Fig. 1). The peatbed in Madurodam was found below Younger Dune sand, whereas the peatbed at Zegbroekpolder occurs at the surface, as a filling of a depression in the Older Dune landscape.

2. THE PEAT-FILLED DEPRESSIONS OCCURRING BELOW THE YOUNGER DUNES

As appears from the map (Fig. 2) the pattern of peatbeds below the Younger Dunes in the area investigated is similar to that of the peat-filled depressions in the Old Dune landscape. The range of peat-bogs running almost parallel to the present coastline reflects the position of former beach plains, which were separated by dune-topped coastal barriers.

In the area of investigation several systems of former beach plains can be recognized. The peat-samples for pollen-analytical and radiocarbon investigation of boring Meyendel–Sparregat were collected in the NW-most system (Fig. 2).

The depths at which peatbeds are found vary a great deal over rather short distances. On the other hand the average depth of the peatbeds in the various localities does not show significant variations, and it is difficult to observe any general tendency in the depth of the peatbeds. In the NW-most range the greatest depth is as a rule found at the NW edge of this system, with a gradual rise to the SE. This is shown in section A–B of Fig. 3. Here the gradual rise of the base of the peatbeds to the SE is interrupted in one place only (near the dune-pan of Bierlap).

In a direction parallel to the present coastline variations in depth are generally smaller and little regularity is to be observed. As an example a section the NW-most peat-depression is given in Fig. 3 (section C–D, location Fig. 2).

In our opinion the greater depth of the peat in the NE part of this section does not reflect a general tendency of lowering of the peat in this direction, for a parallel section situated more inland, shows a rise of the peatlevel towards the NE. In our opinion the shift of section C-D to a more central part of the depression as a result of its broadening near beach mark 93, accounts for the observations made.

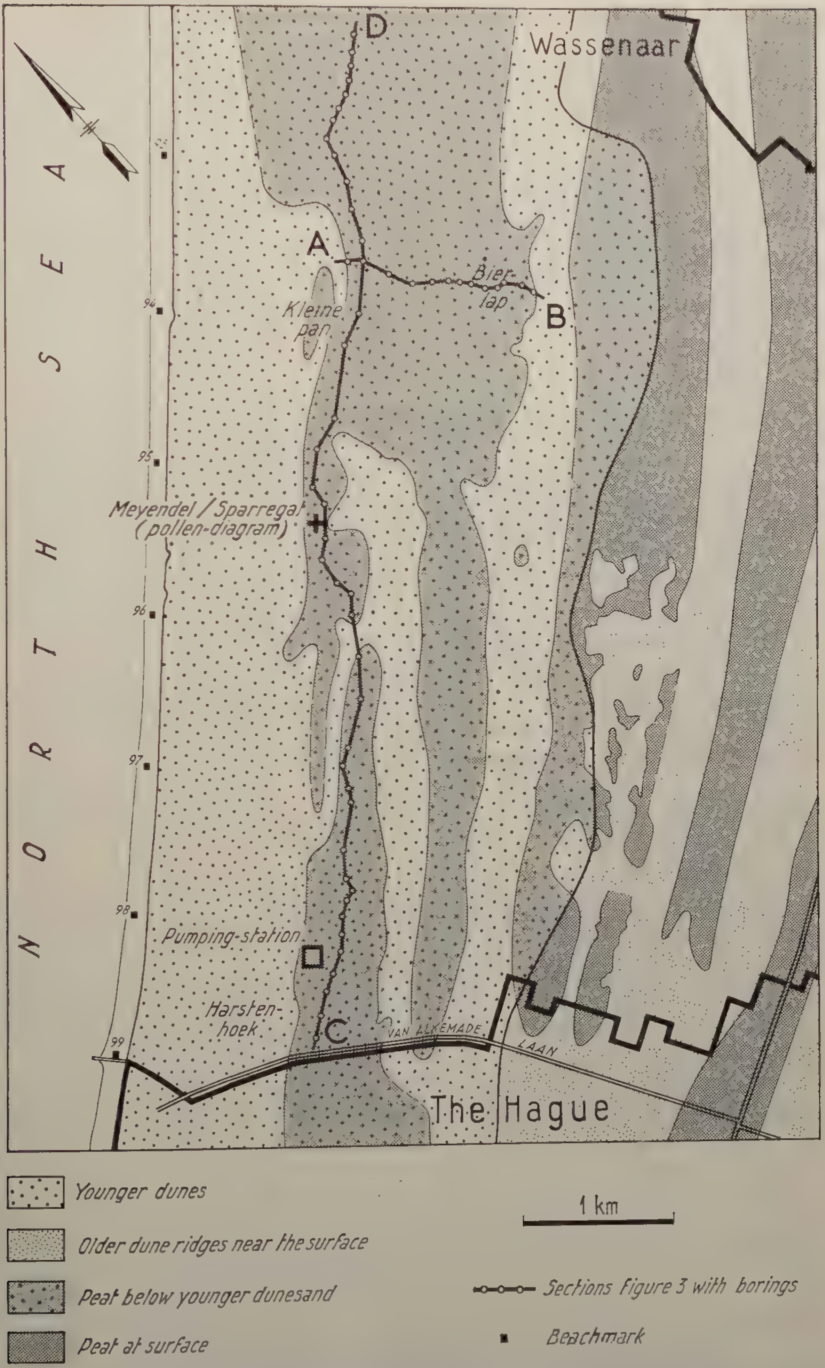

Fig. 2. Map showing repartition of peatbeds in area north of The Hague (location Fig. 1). Location of sections Fig. 3.

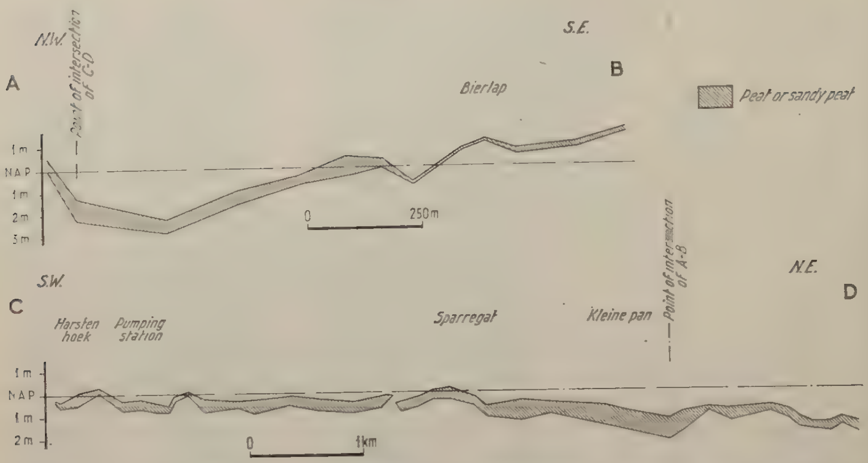

Fig. 3. Cross section A–B and section C–D parallel to coast showing position of peatbeds below Younger Dune sand in area north of The Hague (location Fig. 2).

The thickness of the peat also varies greatly locally. As a rule a thickness of 20–55 cm is found, a thickness exceeding 1 m being exceptional. Along the margins of the peat formations thickness is generally low, increasing towards the centre.

In some cases two, rarely even three, peatbeds are found on top of each other, with dune-sand intercalated between them, pointing to changes in aeolian sedimentation.

3. POLLEN-DIAGRAMS AND RADIOCARBON DATINGS OF SOME PEATBEDS IN THE DUNE AREA

3.1. *Methods*

All samples, studied pollen-analytically, have come from undisturbed cores, taken with the "Dachnowski-sampler". Preparation in the laboratory was executed according to the abbreviated acetolysis method, preceded by boiling with diluted HF. Macroscopic remains have served to determine the kind of peat involved, but samples were not big enough to permit palaeocarpological studies.

As it can be expected that in a coastal dune-area open vegetation has played an important role, at least during some phases of the past, our purpose was to choose a basic pollensum which might give an indication as to the relationships between forest, shrub-vegetation and open landscape in the area. For this reason the pollen-diagrams were not, as is otherwise usual in Holocene sections, based on a tree-pollensum, but on a basic sum comprising trees, shrubs and terrestrial herbs. As much of the sediments examined consisted of reed and sedge peath, local overrepresentation of *Gramineae* and *Cyperaceae* was likely to occur. Therefore their pollen was excluded from the sum, as was also done with pollen and spores of telmatic and aquatic plants.

The main diagram (A) shows the relationship between trees, shrubs and terrestrial herbs. Diagram part B gives the specification of individual pollen-types of these main groups as far as they were considered of special interest. Both diagram A and B have been based on the basic pollensum, comprising 150–200 specimens per sample.

Diagram part C shows the curve of Gramineae and Cyperaceae, based on a pollensum consisting of the basic sum plus Gramineae plus Cyperaceae. Likewise in diagram part D a curve for Dryopteris is given, based on a sum consisting of basic sum plus Dryopteris. This curve is found only in diagram Madurodam, as in the other sections Dryopteris was scarce. Sample numbers according to the files of the Palaeobotanical Laboratory of the Geological Survey will be found at the extreme right of the pollen-diagrams.

3.2. *Pollen-zonation*

The system of pollen-zonation applied at the Geological Survey (Zagwijn, 1959; Jelgersma, 1961) has been used in this paper too (cf. Fig. 7). As changes in the composition of the forests form the basis of this zonation its application in the dune area pertains only to these phases, when forest governed the landscape. Otherwise radiocarbon datings are required to obtain the necessary time-scale.

3.3. *Pollen-diagram Meyendel–Sparregat* (Fig. 4)

A radiocarbon dating of the base of the lower peatbed resulted in an age of about 700 years B.C. The accurate value as well as the sample number of the Groningen laboratory will be found in Fig. 4. All radiocarbon dates have been checked for Suess-effect and therefore the sample-number has been preceded by GRN.

The pollen-diagram of this bed is characterized by fairly high amounts of shrubs and herbs. *Juniperus* and *Hippophaë* are both fairly well represented and may point to prevailing dune-shrub vegetation at that time. *Myrica*, also commonly present, probably inhabited the boggy depressions of the dune landscape. Though the pollen-diagram indicates that at this time no dense forest canopy existed in the vicinity, wooded patches of *Quercus*, *Corylus*, *Alnus* and *Betula* may have occurred.

It is noteworthy that *Fagus* is present in low values only, much lower than in contemporaneous sediments of the coastal area, outside the dunes proper (cf. diagram Zegbroekpolder, Fig. 6); for this reason a pollen-analytical dating is not possible.

Among the herbs *Plantago lanceolata* is well represented. This may point to human influence, as elsewhere, but it should be noted that at present this species is a common inhabitant of natural dune pastures in the coastal area of The Netherlands (Boerboom, 1960). As *Cerealia* are very scarce it seems more likely that the frequency of *Plantago lanceolata* pollen in this bed points to similar conditions then, and not to human influence.

The pollen spectra from the upper peatbed (2–20 cm above sealevel), dated around 300 A.D., show a different picture. Generally speaking, trees are predominant, among which *Quercus*, *Fraxinus*, *Corylus*, *Betula*

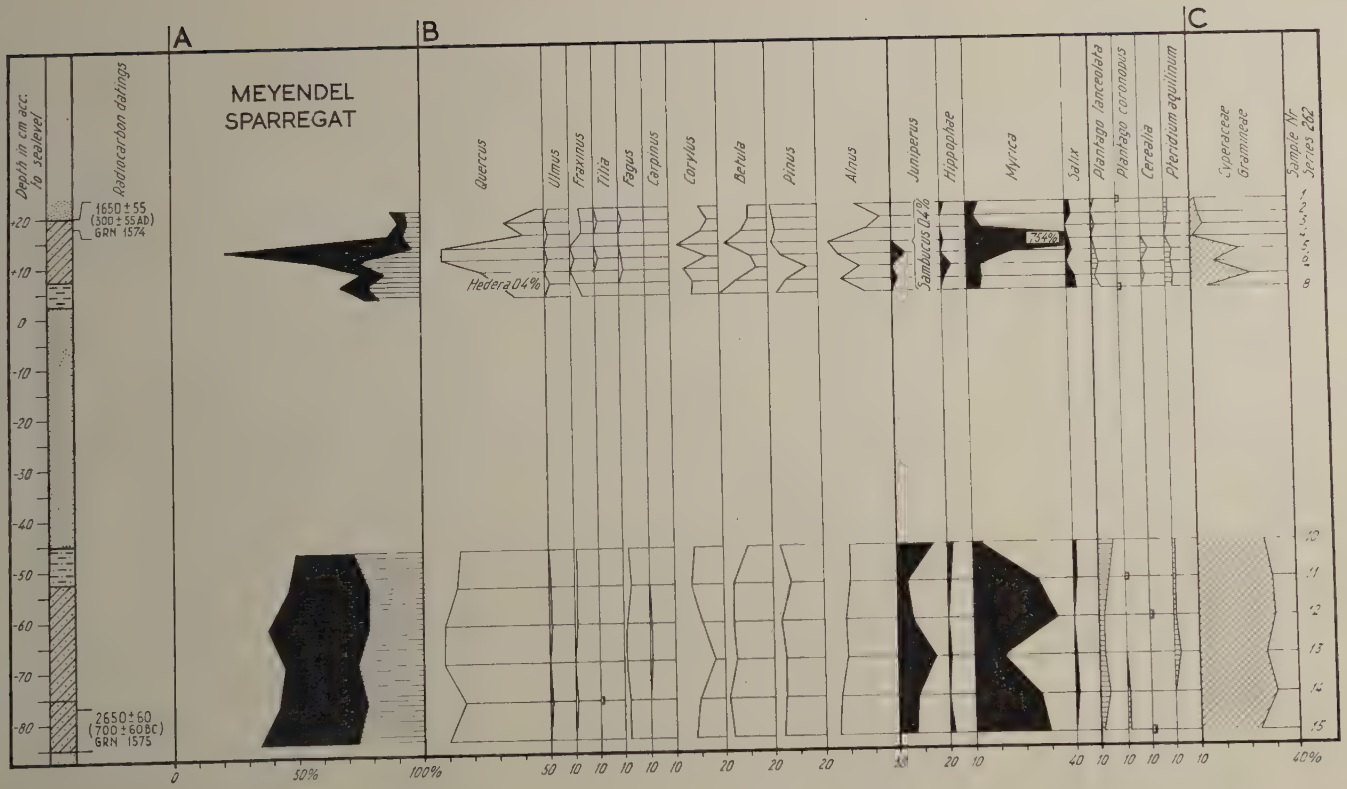

Fig. 4. Pollen-diagram Meyendel–Sparregat (location Figs. 2, 3; legend Fig. 5).

and *Alnus* are most important. *Fagus* is extremely scarce, much scarcer than in contemporaneous diagrams from the inland.

The very high peak of *Myrica* in the middle of the bed is considered a local feature only. Dune shrubs (*Juniperus*, *Hippophae*) are but scarcely represented, mostly in the lower part of the bed. A similar trend is shown by the curve of *Plantago lanceolata*.

In the middle of the peatbed human influence can be traced in the diagrams by a maximum of *Cerealia* at ± 10 cm and perhaps also by the marked decrease in *Quercus* and increase in *Betula* and *Corylus* around this level. These are features well-known from pollen-diagrams of the "landnam"-type (IVERSEN, 1941), though, it is true that the phenomenon is largely obscured in the pollen-diagram discussed here by the strong local expansion of *Myrica* just above this level.

3.4. *Pollen-diagram Madurodam* (Fig. 5)

Even though no radiocarbon datings are available, it is likely that this peatbed roughly dates from the same period as those of Meyendel. The basal spectrum obtained from humic sand shows very high values for *Hippophaë* and *Juniperus*. Evidently dunal shrub formed the main vegetation in this area then. The next few spectra (240–255 cm below surface) show a picture similar to that shown by the upper peatbed at Meyendel: rather dense forest as evidenced by the relatively high values of tree-pollen, but still some traces of dunal shrub. *Fagus* is still rather scarce, however. Presumably this part belongs to pollen-zone V a.

The uppermost two spectra likewise show a prédominance of trees, but now *Juniperus* and *Hippophaë* are absent. Moreover *Fagus* and *Carpinus* are fairly well represented, which definitely points to pollen-zone V b. As furthermore *Cerealia* of the *Secale*-type show high values, a more precise attribution to sub-zone V b_2 (± 700 A.D.–± 1200 A.D.) is possible. The presence of *Centaurea cyanus* in the uppermost sample moreover indicates a fairly late dating within this sub-zone, say around 1200 A.D.

3.5. *Pollen-diagram Zegbroekpolder* (Fig. 6)

A gyttja-filling 160 cm thick found in the third peat-filled depression south of The Hague and occuring outside the Younger Dune area, has been investigated pollen-analytically.

The base of the deposit was fixed by radiocarbon dating at about 1200 B.C. (JELGERSMA, 1961). Another point of reference is found in the level of 50–60 cm below surface, which pollen-analytically can be shown to represent the level of the Dunkirk I transgressional phase, elsewhere dated around 500–250 B.C. (VAN STRAATEN, 1957).

The spectra from the base of the deposit show high amounts of trees (*Quercus*, *Alnus*) and it is likely that forest prevailed in the area. The fact that *Fagus* is represented in values of about 1–2 % points to the second half of the Subboreal, pollen-zone IV b, which is in good agreement with the radiocarbon dating. From 130 cm below surface upwards an increase of shrub-vegetation can be observed especially

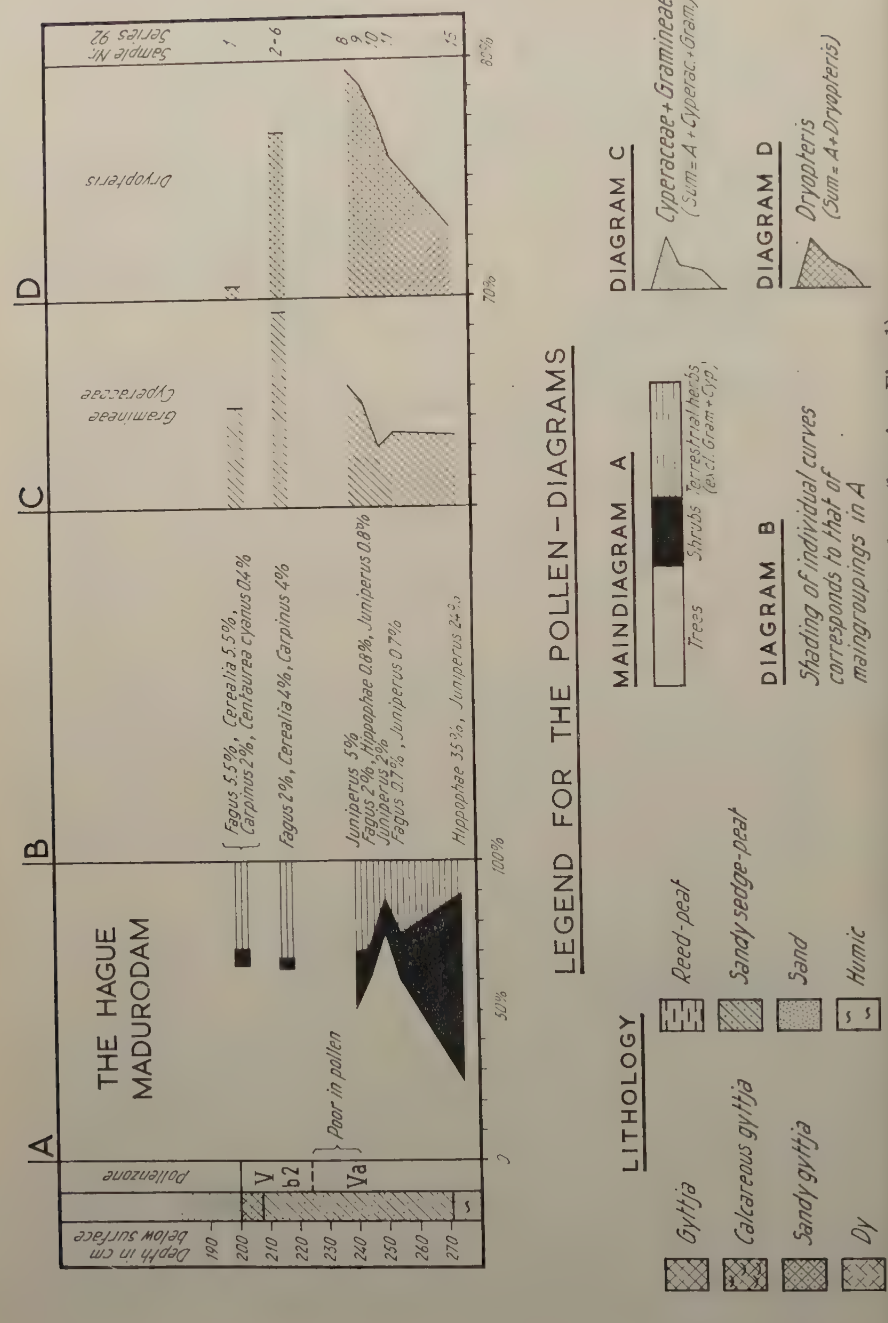

Fig. 5. Pollen-diagram Madurodam (location Fig. 1).

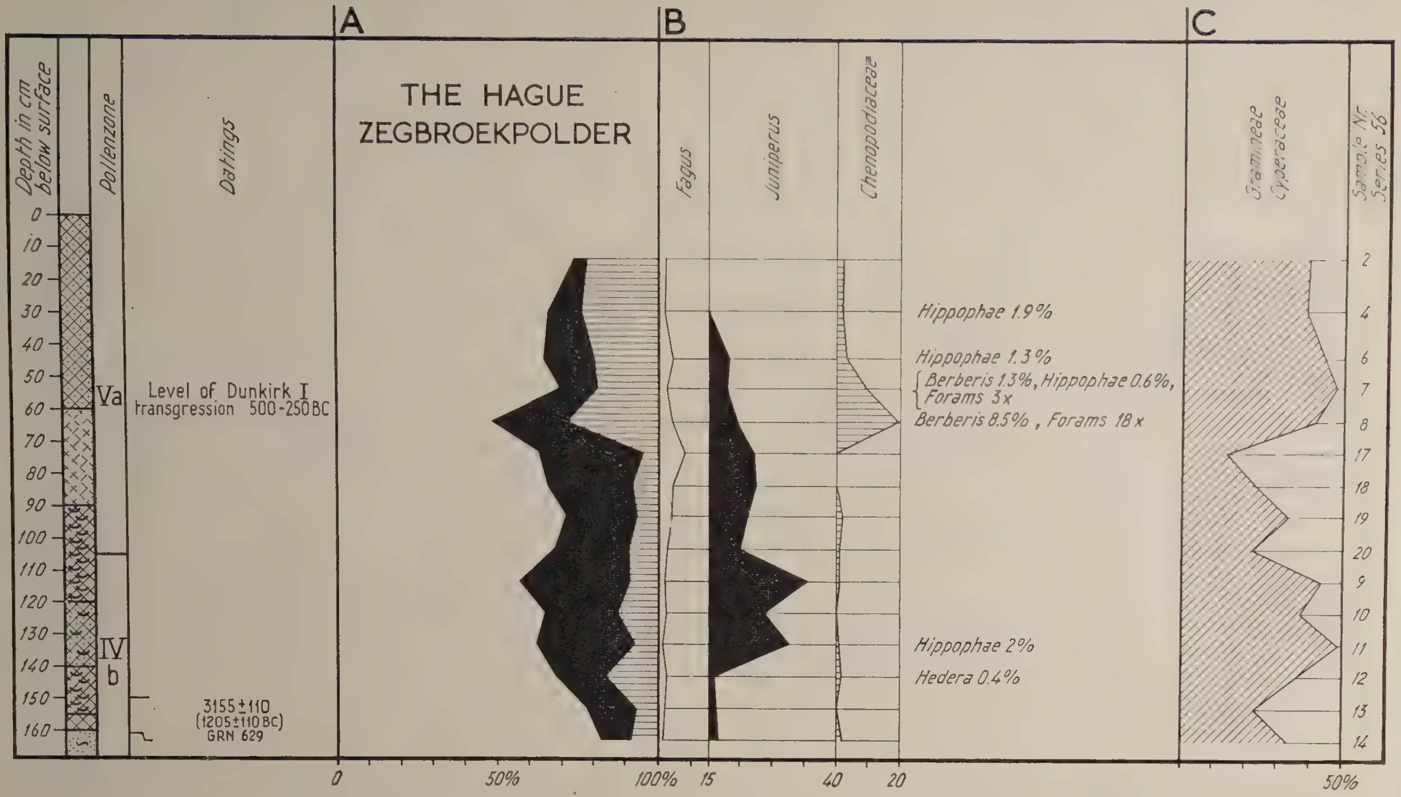

Fig. 6. Pollen-diagram Zegbroekpolder (location Fig. 1; legend Fig. 5).

of *Juniperus*, together with an increase in sandiness of the beds. It might be inferred that in the area forest was partly replaced by a dune-shrub vegetation. Higher up in the diagram the percentages of shrub-pollen gradually decrease again and the topmost spectrum does not show traces of dune shrubs anymore. The trend of the *Fagus*-curve, showing a rise about halfway the diagram, points to deposition during pollen-zone V a (first half of Subatlantic) of the part 0–100 cm of the deposit. In this connection it should be noted that the level 40–60 cm below surface shows a marked increase in *Chenopodiaceae*, as well as the occurrence of *Foraminifera*. The level thus shows a temporary change to saltwater conditions of the otherwise fresh environment. Now in the coastal areas of the western Netherlands a marked transgression phase can be observed within pollen-zone V a (ZAGWIJN, unpublished; JELGERSMA, 1961), which is identical with the well-known "Pre-Roman" or Dunkirk I phase (VAN LIERE, 1948; BENNEMA, 1954; TAVERNIER, 1954; PANNEKOEK, 1956). From this it can be concluded that the marine influence found in the Zegbroekpolder marks the ingression of the sea in this depression during the Dunkirk I phase.

A comparison of this diagram with those of the contemporaneous beds at Meyendel and Madurodam shows that in the latter localities the values for shrubs and herbs are generally higher than at Zegbroekpolder. Probably there the character of the dune landscape was more distinct.

4. CONCLUSIONS

The pollen-diagrams from peatbeds below Younger Dune sand in the area north of The Hague (Meyendel, Madurodam) indicate that in Early Subatlantic times an open dune-shrub vegetation with *Juniperus* and *Hippophaë* was predominant, which was gradually replaced by oak-forest in the first centuries A.D. Deposition of Older Dune sand took place up to this time. Later, at least locally, *Fagus* and *Carpinus* expanded in this forest. Pollen-analysis of the Madurodam section, which is near the eastern limit of the Younger Dunes, indicates that their formation in this area took place at least after 700 A.D., probably even after 1000–1200 A.D. No pollen-data are as yet available to give an impression of vegetation prevailing during the formation of the Younger Dune sands.

This rather late dating of the beginning of Younger Dune formation is in good accordance with a number of archaeological datings from other areas (BRAAT, 1947; TRIMPE BURGER, 1960).

The pollen-diagram Zegbroekpolder from the area south of The Hague indicates prevailing forest in Late Subboreal times and presumably a standstill of aeolian deposition, expansion of duneshrub at the Subboreal-Subatlantic boundary and subsequently reafforestation in the centuries preceding the beginning of our era. On the whole the dunal character of vegetation in the period discussed is less distinct than in the area north of The Hague.

Perhaps this can be attributed to a greater distance from the former coastline, though perhaps also the vicinity of the estuary of the Meuse (the Helinium of Roman times) may have played a role, where groundwater conditions may have been more conducive to the preservation of forest than in drier areas farther away from the river-mouth. As to the character of the dune vegetation it can be remarked that the pollen-diagrams presented in this paper only reflect the presence of dune-shrub. In contrast to such communities found in the present Younger Dunes, which are rich in lime, not only *Hippophaë* has been found but commonly also *Juniperus*. This, together with the presence of *Pteridium* and *Myrica*, points to a less calcareous character of the Old Dune sand.

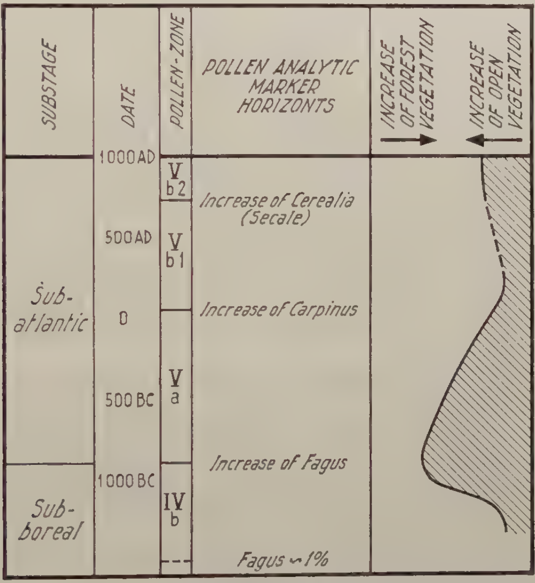

Fig. 7. Table of Late Holocene vegetational history in Dune area of The Hague, as compared with time-scale and pollen-zonation.

In Fig. 7 the conclusions discussed here concerning the alternation of forest and open dune vegetation in this area have been graphically schematized as compared with the pollen-zonation and absolute datings.

ACKNOWLEDGEMENTS

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The authors are indebted to the Netherlands Organization for the Advancement of Pure Research (Z.W.O.) for granting funds to make the radiocarbon datings possible.

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THE OCCURRENCE OF *SALVINIA NATANS* (L.) ALL. IN HOLOCENE DEPOSITS OF THE RHINE DELTA

K. J. ZANDSTRA

(*Laboratory of Regional Soil Science, Agricultural University, Wageningen, the Netherlands*)

(*received January 26th, 1966*)

Introduction

Salvinia natans is a warm temperate species still living in Europe (Map 1). Up to 1936 it was only known from Pleistocene interglacial deposits. Florschütz and Jonker (1936) first mentioned it in 1936 in post-glacial deposits; only one macrosporangium was found in the Holocene underneath the Cathedral Square at Utrecht. In 1939 the same authors discovered large amounts of macro- and microsporangia in an Old Atlantic clay near Wijk bij Duurstede (Map 2).

According to Godwin (1956), up to that year these were the only occurrences known from the west European Post-Glacial.

However, in 1961 Jelgersma gave a diagram from Alphen-on-the-Rhine, in the delta region, where microsporangia of *Salvinia natans* had been encountered in gyttja and dy from the Atlantic period (Map 2).

Finally, the present author has added a new find, also from the Atlantic, in the same region of the Rhine delta (Map 2 and Fig. 1).

In view of the now known sites of occurrence, it would therefore appear likely that *Salvinia natans* had a natural habitat in the Rhine delta in the Atlantic. Hence it is by no means impossible that this species, which requires a warm temperate climate, may be encountered in other river clay regions in the same environment and period.

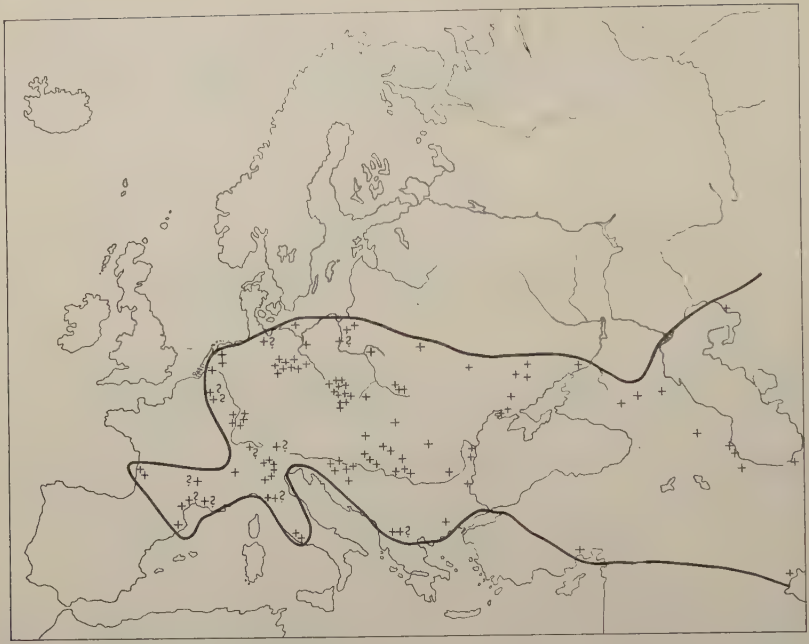
The find-place of Salvinia natans in 1965

In 1965 the author sampled a profile in the Vuylcop polder in connection with an investigation into the Utrecht river area. This polder is situated between the Houten- and the Linschotensystem, former arms of the river Rhine (map in Vink, 1926 and 1954).

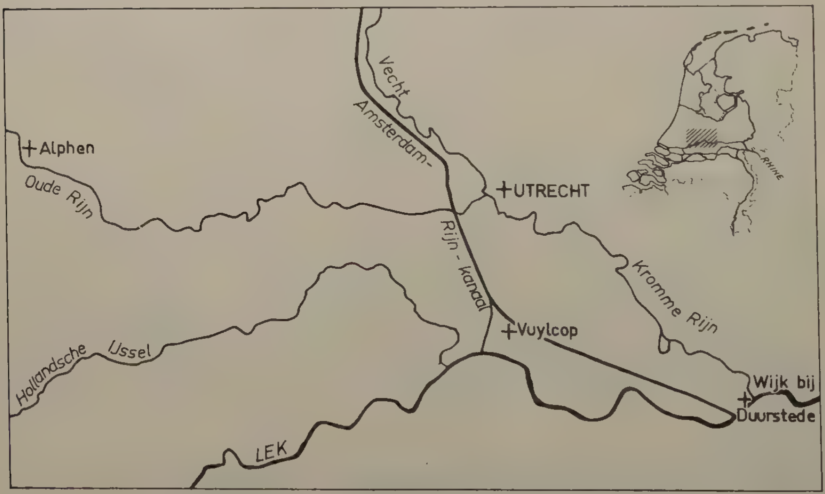
The samples were collected near the Hoonrug, a silted up stream-channel. The site is located to the south of the Amsterdam-Rhine Canal, midway between the 46 and 47 km marks, east of the ferry to Houten, in a meadow about 2 m past the berm ditch (Map 2).

The profile

0– 60 cm	backswamp clay disturbed by excavation
60– 83 cm	backswamp clay
83–100 cm	black, tight, buried soil horizon
100–110 cm	humose backswamp clay



Map 1. Distribution of *Salvinia natans* (L.) All. in Europe (after Hegi).
+ ? = Fossil



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Map 2. Part of the Rhine delta with location of *Salvinia* finds (+)

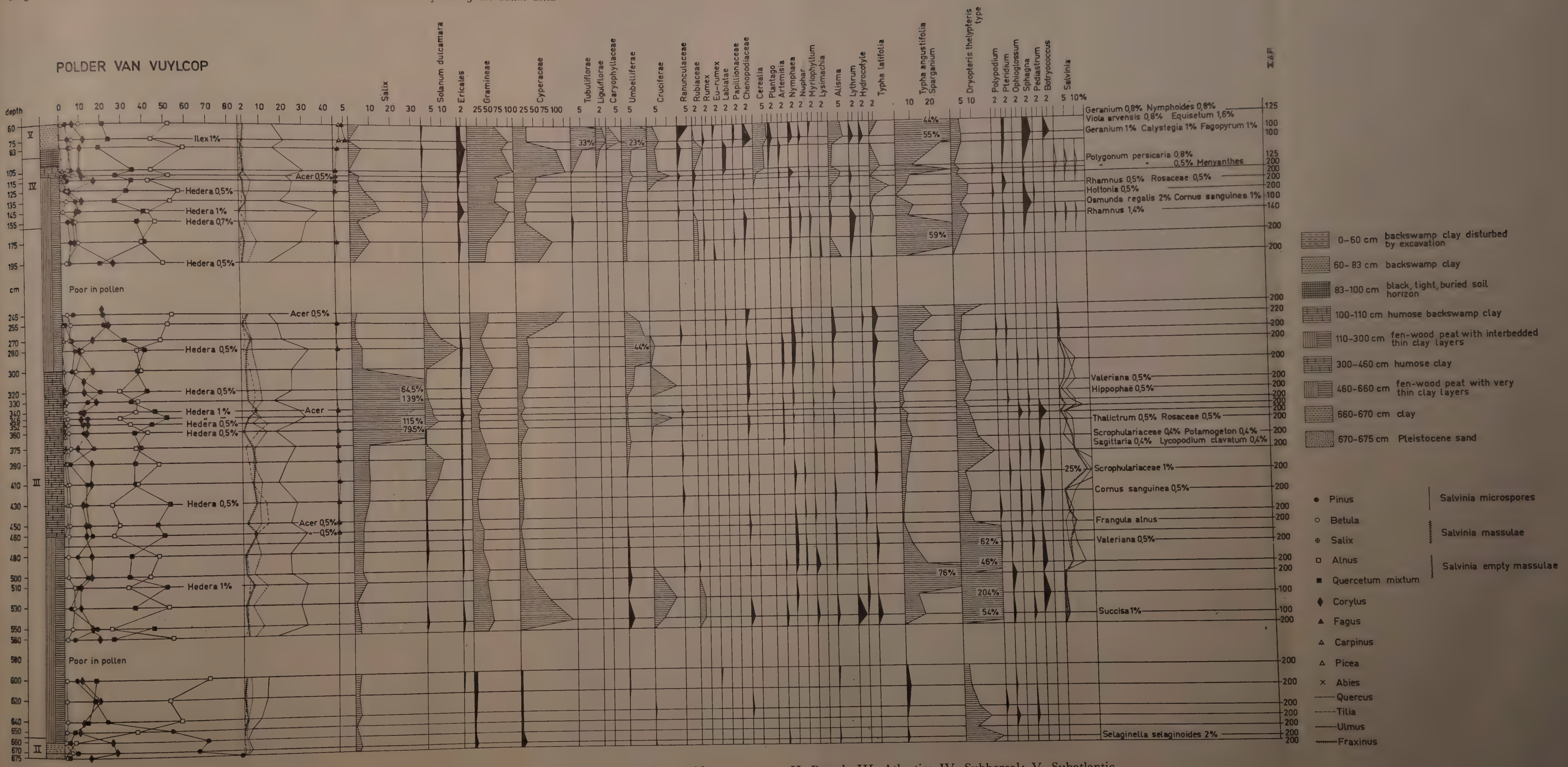
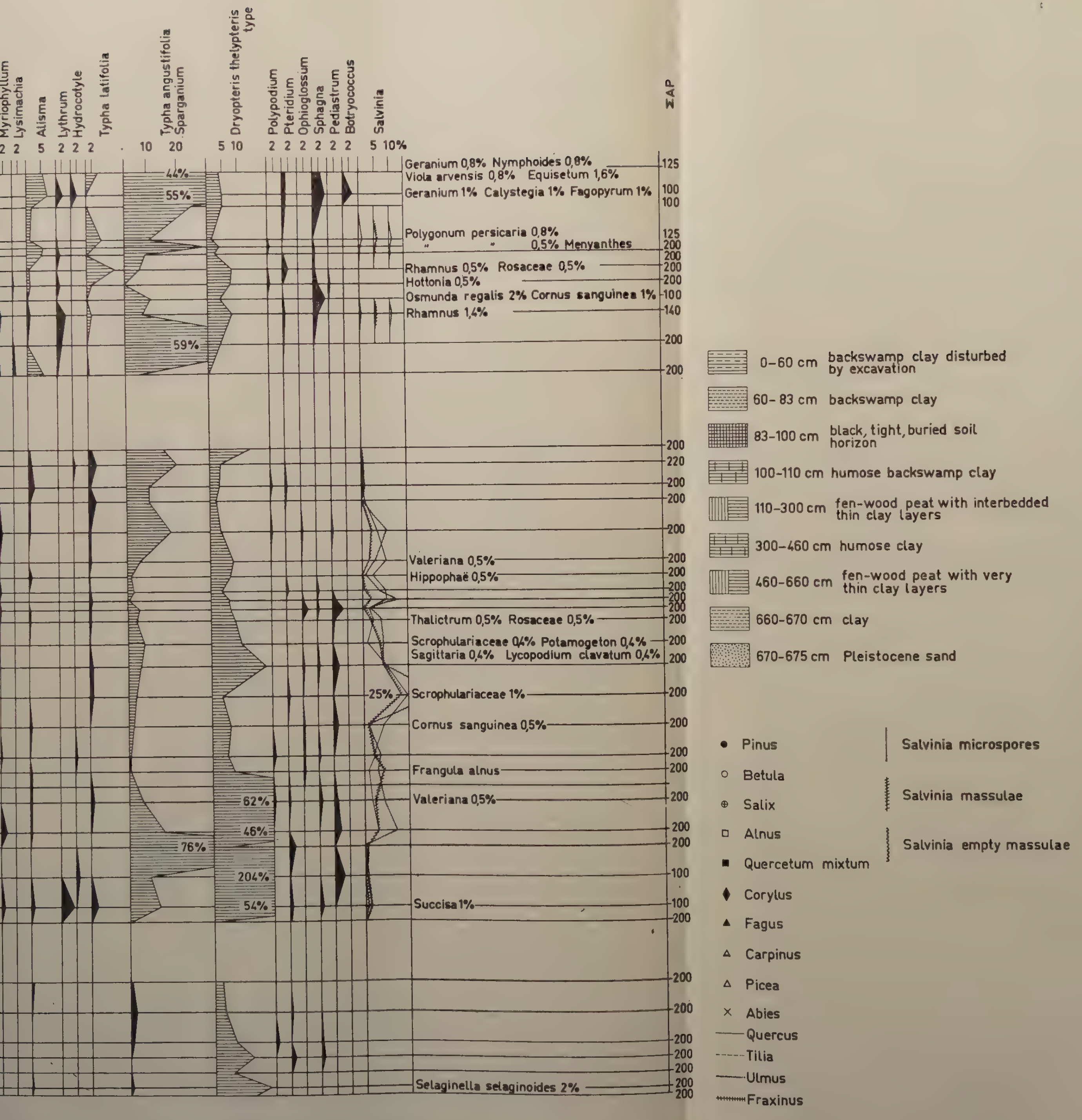


Fig. 1. Diagram of the Vuylcop polder. II. Boreal; III. Atlantic; IV. Subboreal; V. Subatlantic



oreal; III. Atlantic; IV. Subboreal; V. Subatlantic

110–300 cm fen-wood peat with interbedded thin clay layers
300–460 cm humose clay
460–655 cm fen-wood peat with very thin clay layers
655–670 cm clay
670–675 cm Pleistocene sand.

The layer of clay overlying the sand belongs to the fluvial Low-Terrace of BENNEMA and PONS (1952). It was also observed by VINK (1926) and DE BOER and PONS (1960). A cross section showed the 300–460 cm layer to be a wedge of clay originating in the Hoornrug (cf. Fig. 4, DE BOER and PONS, 1960). This wedge was particularly rich in remains of aquatic plants, including the water fern *Salvinia natans*. The black layer (83–100 cm) is a fire layer and hence deficient in pollen.

POLLEN ANALYSIS

A number of particular difficulties are involved in the pollen analysis of specimens from the river clay area.

The Rhine brings down pollen from its upstream area and may deposit it in the Utrecht basins. Thus several slides contain pollen of *Abies* and *Picea* which do not belong to the Post-Glacial native flora, although both general occurred in the Alpine forelands, the Vosges and the Black Forest, FIRBAS (1949).

The clay wedge samples contain small percentages of *Fagus* pollen in the Atlantic period. To a lesser extent S. JELGERSMA (1961) found the same in the coastal area. Since the beech is not a native of the Netherlands Atlantic period it would seem likely that in this case it was brought down by the Rhine. In the Old Atlantic beeches were a considerable feature of the upstream area of the Rhine, FIRBAS (1949).

At the same time, however, we should not overrate the possibility of pollen grains being brought down by the Rhine. The pollen composition of the samples indicates a well-developed local vegetation.

Evidence of the local deposition of pollen of such aquatic and marsh plants as *Alnus*, *Typha*, *Gramineae*, *Cyperaceae*, etc. is to be found in the occurrence of clods of pollen that would certainly have become detached if carried by the stream. The occurrence of stellate hairs of *Nymphaea* and rootlets of *Gramineae* and *Cyperaceae* is also self-explanatory in this connection.

The possibility of *S. natans* in the Atlantic period being carried down from the upper Rhine areas is to be precluded for the following reasons: firstly, the fragile, reticulated sporangium wall was often intact and it is unlikely that this could have withstood long transport by water; secondly, the occurrence of *S. natans* is limited to the Atlantic period.

THE DIAGRAM

$\sum$ A.P. The records are based on 200 tree pollen per spectrum, but this figure could not be reached in some layers with a high percentage of charcoal (fire layers) owing to the lack of, or severe corrosion of the pollen grains. *Salix* was excluded from the $\sum$ A.P. owing to overpresentation.

$\sum$ N.A.P. The numbers of pollen and spores of herbs were calculated at percentages of $\sum$ A.P.

Of *Salvinia natans* there were counted in the slides:

a. massulae (hardened rounded alveolate mass with maturing spores);
b. empty massulae (without spores);
c. microspores.

Moreover a large number of macro- and microsporangia have been obtained by washing from the clay.

ENVIRONMENT

Aquatic and marsh plants may be classified in six different types of vegetation, depending on the water level WESTHOFF *et al.* (1946):

1. *Potamion*, plants growing in water less than 4 m deep: *Salvinia natans*, *Potamogeton*, *Nymphaea*, *Nuphar*, *Menyanthes*, *Hottonia*, *Nymphoides*, *Myriophyllum*, *Pediastrum*.
2. *Phragmition*, plants growing in water 2–0.25 m deep: *Typha*, *Alisma*, *Sagittaria*.
3. *Magno-caricion*, plants growing in water 0.25–0 m deep: *Cyperaceae*.
4. *Filipendulo-petasition*, water level 0 m. Herbs, no woody species, *Filipendula*, *Lythrum*, *Lysimachia*, *Succisa*, *Hydrocotyle*, *Valeriana*. *Thalictrum*, *Eurumex*.
5. *Alnion*, water level 0 m. Alternately wet and dry. In combination with woody species. *Solanum dulcamara*, *Ophioglossum*, *Osmunda*, *Dryopteris thelypteris*.
6. *Salicion*, water level 0 m. Alternately wet and dry. A preference for mineral soils. *Salix spec.*

As the diagram of the Vuylcop polder shows, *S. natans* belongs to the *Potamion*.

The relative fall in the water level caused by the sedimentation of river clay changed the character of the vegetation. At the same time there was a fall in the discharge of the Hoonstroom, with the result that river water was only occasionally brought down to the basin. Peat growth occurred, but bands of clay are still visible in the peat. At some periods there was enough water in the basin for the sporadic appearance of *S. natans*, but in increasingly smaller numbers. At the end of the Atlantic the climate gets unfavourable for *S. natans*.

The environment of *S. natans* in JELGERSMA and FLORSCHÜTZ and JONKER is given below for comparison.

In JELGERSMA's (1961) diagram we find *Nymphaea*, *Nuphar*, *Typhaceae*, *Myriophyllum*, *Sagittaria* and *Potamogeton* in the *S. natans* range.

No herb pollen is included in the FLORSCHÜTZ and JONKER (1939) diagram, but fruits, leaves and seeds are shown. In the layer in which *S. natans* occurs we again encounter *Nymphaea*, *Nuphar*, *Potamogeton*, *Alisma*, *Sparganium*, *Chara* and *Batrachium*, together with *Phragmites*.

It will be seen from the above that *S. natans* occurs in the same type of vegetation in three out of four find-places. The water fern prefers stagnant eutrophic water 2 to 4 m in depth. The Atlantic supplied the need of a warmer climate than that prevailing today.

At present *S. natans* does not occur north of the upper Rhine area, but it is occasionally transported thence to Holland by wood drafts and sometimes maintains itself for several decades FLORSCHÜTZ and JONKER (1939).

CONCLUSION

In the delta areas of the Rhine *Salvinia natans* occurred in three different diagrams during the Atlantic. Entire massulae, macro- and microsporangia have been found; in particular, the intact, foamlike network of massulae, their large numbers and the long period over which they are found, would make local growth appear extremely probable, as also the correspondence with the environment. This is a fairly deep basin, rich in eutrophic water plants, in which a gradual silting-up occurs.

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THE INFLUENCE OF LIGHT OF DIFFERENT SPECTRAL REGIONS ON THE SYNTHESIS OF PHENOLIC COMPOUNDS IN GHERKIN SEEDLINGS IN RELATION TO PHOTOMORPHOGENESIS

III. HYDROXYLATION OF CINNAMIC ACID

G. ENGELSMA

(*Philips Research Laboratories, N.V. Philips' Gloeilampenfabrieken,*
Eindhoven – Netherlands)

(*received October 24th, 1965*)

Abstract

1. Light stimulates the conversion of L-phenylalanine and of trans-cinnamic to p-coumaric acid in hypocotyl segments from dark-grown gherkin seedlings.
2. Inhibition by cycloheximide of the increase in the rate of hydroxylation of cinnamic acid in response to light indicates that *de novo* synthesis of enzyme, probably cinnamic acid hydroxylase, is involved.
3. The responsivity to light is higher in the apical part than in the basal part but the spectral sensitivity does not alter significantly over the length of the hypocotyl. The photoreceptor directly responsible for the effect of blue light seems to be different from phytochrome.
4. Particularly in red and far-red light an effect of the cotyledons on the hydroxylase activity to be obtained in the hypocotyls becomes apparent.
5. There is a general correlation between the influences of light quality, light intensity and duration of irradiation on the hydroxylase activity and the accumulation of hydroxycinnamic acids in the gherkin hypocotyl.
6. The implications of this photo-inducible reaction for the regulation of lignification and cell elongation are discussed.

1. Introduction

The photocontrol of the accumulation of hydroxycinnamic acids in the hypocotyls of gherkin seedlings shows characteristics which are typical of several other light-dependent developmental processes in plants (Engelsma and Meijer, 1965a). The biosynthesis of these phenols seems well suited for a study on the mechanism of light action in photomorphogenesis because of the relative simplicity of this phenomenon. Fairly detailed knowledge about the metabolic pathway is already available (Neish, 1964).

Feeding experiments with trans-cinnamic acid and glucose enable us to study the influence of light on only a small part of this pathway, the synthesis of the glucose ester of p-coumaric acid from these compounds. In investigations carried out with segments from the gherkin hypocotyl we have tried to find an answer to the following questions.

1) In how far does hydroxylation of cinnamic acid play a key role in the light-dependent accumulation of hydroxycinnamic acids in the hypocotyl of intact seedlings? An enzyme responsible for this reaction, cinnamic acid hydroxylase, has been demonstrated by Nair

and Vining (1965) in spinach leaves. The question is whether there is a correlation between the effects of light on the hydroxylase activity and the accumulation of phenols.

2) Besides phytochrome, are there other pigments involved in this process? If there are different photoreceptors with different distribution patterns, experiments with segments cut from various parts of the hypocotyl could supply an answer to this question.

3) Is the effect of light translocated intercellularly or does the site of ultimate response always coincide with the site of light perception? This can possibly be solved by varying on the one hand the part of the plant which is irradiated, and on the other hand the interval between light treatment and excision of the segment.

In view of the close connection between phenol synthesis, lignification and cell elongation (Engelsma and Meijer, 1965b) changes in hydroxylase activity are expected to have an important bearing on the latter two phenomena too. A preliminary account of some of the results has been published elsewhere (Engelsma, 1965).

2. Methods and materials

The experiments were carried out with segments excised from the hypocotyls of gherkin seedlings (*Cucumus sativus*, "Venlose niet plekkers", strain Tercken VI) raised as described before (Engelsma and Meijer, 1965a). Unless otherwise stated 5 mm segments were used which were cut with the aid of a mechanical device immediately below the plumular hook of three-days-old dark-grown seedlings. All manipulations were carried out under dim green safe-light obtained with a fluorescent lamp (Philips "TL" 17) filtered with "Plexiglas" yellow No. 3 and "Cinemoid" Nos. 39 and 16. Usually the experiments were performed in petri dishes with lots of 30 segments which were floated on 10 ml of distilled water or precursor solution. The latter consisted of an aqueous solution of 10^{-3} M trans-cinnamic acid (BDH) or another p-coumaric acid precursor and 1 % glucose at pH 5.0. The glucose was added as a routine in order to avoid that this compound might become rate-limiting. Irradiations were carried out at 25° C with the same light and filter combinations as used previously (Engelsma and Meijer, 1965a). The p-coumaric acid glucose ester was determined spectrophotometrically as described in the same paper. All data refer to segments kept in the precursor solution for 24 hours at 25° C. Calculations are based on a molar absorbance of 3.10^4 cm^2/mmole at 350 mμ for the ester at pH > 10.0. Each point in the graphs represents the mean of at least three experiments, each run in duplicate.

3. Results

Precursors of p-coumaric acid biosynthesis

In the hypocotyls of gherkin seedlings two hydroxycinnamic acids are synthesized, p-coumaric acid and ferulic acid (Engelsma and

MEIJER, 1965a). Light stimulates the synthesis of these compounds. It is generally accepted that in higher plants the aromatic compounds are formed via the shikimic acid pathway (NEISH, 1964). We tested a number of potential precursors for their ability to increase hydroxycinnamic acid synthesis in hypocotyl segments from gherkin seedlings. The results are presented in Table 1. Segments were floated on the precursor solution, and kept in darkness for 24 hours, or were irradiated with blue light (700 μW/cm^2) for 8 hours and subsequently kept in darkness for 16 hours. Only phenylalanine and trans-cinnamic acid gave a clear increase in phenol synthesis. The effect was stimulated by blue light. The same was found for red and far-red light but this part of the spectrum proved to be less effective.

TABLE 1

Effect of different metabolites of the shikimic acid pathway on the synthesis of hydroxycinnamic acids, mainly glucose ester of p-coumaric acid, in gherkin hypocotyl segments during 24 hours in darkness and during 8 hours in blue light (700 μW/cm^2) followed by 16 hours of darkness. All solutions at pH 5.0 with NaOH. Numbers are mμmoles of hydroxycinnamic acid/segment

Solution:	24D	8B16D
Water	1.0	5.0
1 % Glucose	1.4	5.1
Quinic acid (10^{-3} M) + 1 % glucose	1.3	4.8
Shikimic acid (10^{-3} M) + 1 % glucose	1.7	5.0
Phenyllactic acid (10^{-3} M) + 1 % glucose	2.0	6.0
L-Phenylalanine (5×10^{-3} M) + 1 % glucose	2.7	12.5
Tyrosine (10^{-3} M) + 1 % glucose	1.7	5.8
trans-Cinnamic acid (10^{-3} M) + 1 % glucose	8.3	29.7
p-Coumaric acid (10^{-3} M) + 1 % glucose	3.5	11.4

Surprisingly, quinic acid and shikimic acid, which were found to be precursors in the synthesis of aromatic compounds in a number of plants (NEISH, 1964), did not cause any significant stimulation in our system. The compounds were tested over a range of different concentrations, acidities of the medium and light conditions, but the possibility can not be excluded that they fail to stimulate phenol synthesis in the gherkin hypocotyl because they do not reach the active site.

Optimal phenol synthesis was obtained at concentrations of 5×10^{-3} M L-phenylalanine or 10^{-3} M trans-cinnamic acid respectively. These compounds are almost exclusively converted to the glucose ester of p-coumaric acid, very little ferulic acid being formed. Cycloheximide (5 μg/ml) and chloramphenicol (2 mg/ml) block the light stimulation, indicating that *de novo* enzyme synthesis is involved (ENGELSMA and MEIJER, 1965a; ENGELSMA, 1965).

Distribution of the light sensitivity

An important problem in photomorphogenesis is to what extent other pigment systems besides phytochrome are involved. In the hope that if the effects of different wavelength regions are mediated through different pigment systems these systems might not be equally distributed, we excised segments from different parts of the hypocotyl to determine the distribution of the spectral sensitivity for the induction of enzyme synthesis. From three-days-old dark-grown seedlings three segments were cut: the plumular hook, about 5 mm in length, a segment, 5 mm long, immediately below the plumular hook, and a segment, 5 mm long, about 5 mm above the implantation of the roots. The segments received the light treatment during 24 hours while floating on the cinnamic acid, glucose solution.

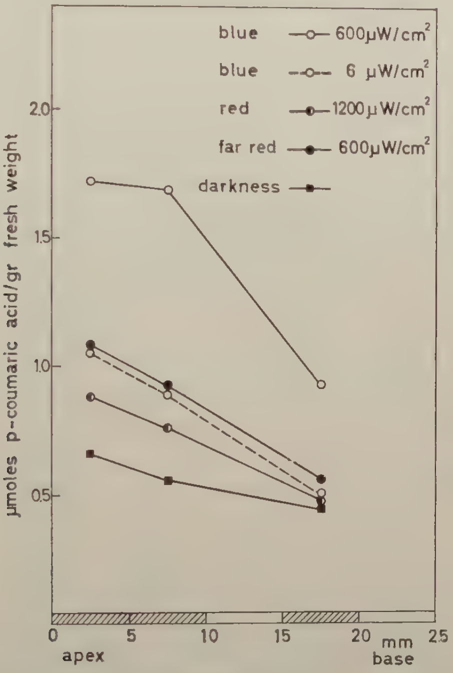

Fig. 1. Hydroxylation of cinnamic acid induced by continuous irradiations for 24 hours with blue, red and far-red light respectively in segments excised from different parts of the hypocotyls from dark-grown gherkin seedlings.

The results presented in Fig. 1 show that in segments kept in the dark the capacity to convert cinnamic acid into p-coumaric acid decreases from apex to base. This pattern remains the same in the light-treated segments. Blue light is much more effective than red and far-red light but there is no clear evidence that the distribution of the sensitivity for this light is different from that for the other spectral regions. If different pigments are involved, they must be rather equally distributed.

Dependence of light quality, light intensity and duration of irradiation

The influence of the duration of irradiation in blue, red and far-red light on the hydroxylation of cinnamic acid in hypocotyl segments

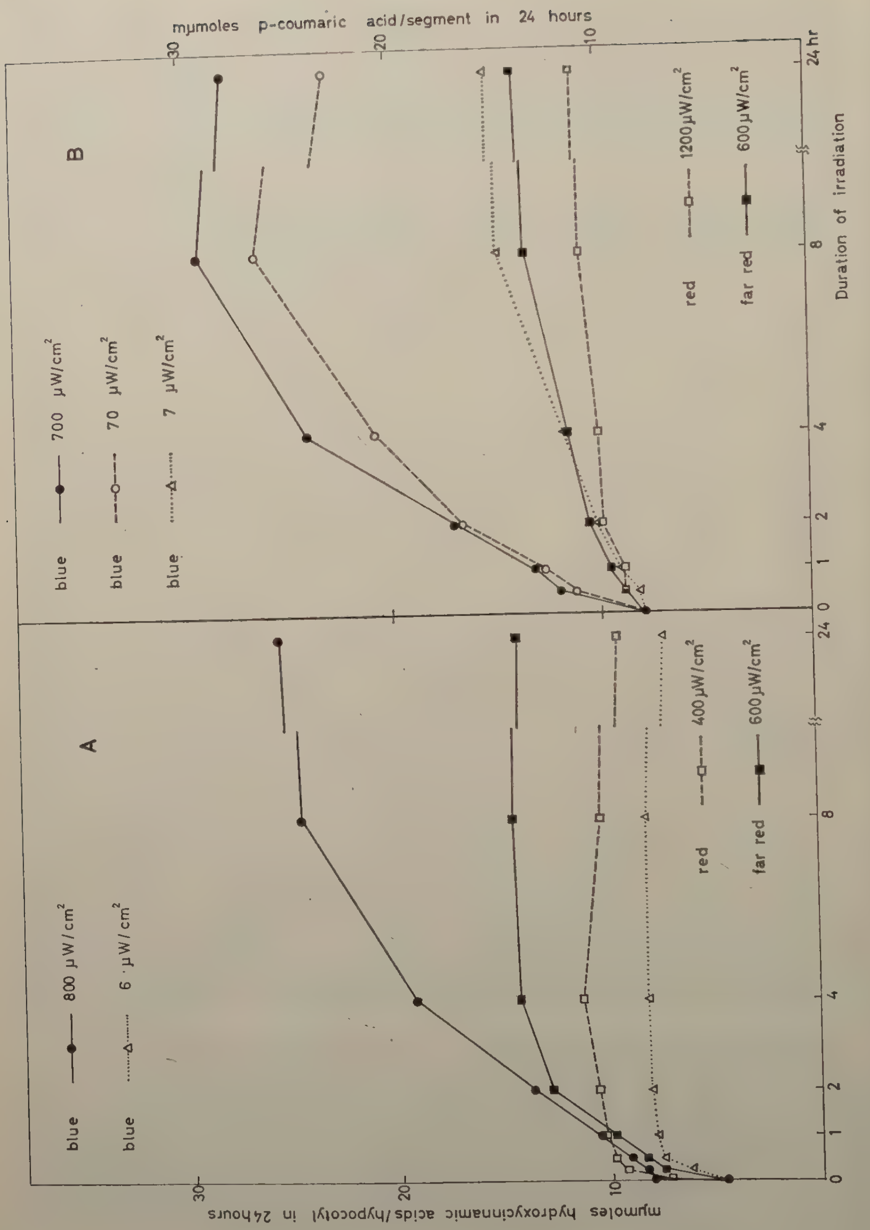

Fig. 2. Phenol synthesis as a function of the duration of irradiation with blue, red and far-red light in the hypocotyls of intact seedlings (A) and in hypocotyl segments floated on an aqueous solution of 10^{-3} M trans-cinnamic acid and 1 % glucose (B).

is given in Fig. 2B. Lots of 30 segments were floated on aqueous solutions of 10^{-3} M trans-cinnamic acid and 1 % glucose (pH 5.0), irradiated for the times indicated in the graphs, and subsequently kept in darkness until 24 hours from the beginning of the light treatment. In a number of aspects the results are remarkably parallel with those relating to the effects of light on the accumulation of hydroxycinnamic acids in hypocotyls of intact seedlings (Fig. 2A) (Engelsma and Meijer, 1965a). Particularly in blue light we find the same dependence on light intensity and duration of irradiation. Saturation occurs after about 8 hours of irradiation irrespective of light intensity. On the other hand very short irradiations, especially with blue and red light, have a relatively marked effect on phenol accumulation in the hypocotyls of intact plants whereas the effect on the hydroxylase activity in segments is negligible. Moreover, also for irradiations of longer duration the relative effectiveness of red and far-red light is much lower in the latter case. Their influence on the induction of hydroxylase activity in segments reflects rather the induced phenol synthesis in the hypocotyls of decotyledonized plants than in those of intact plants (Fig. 3).

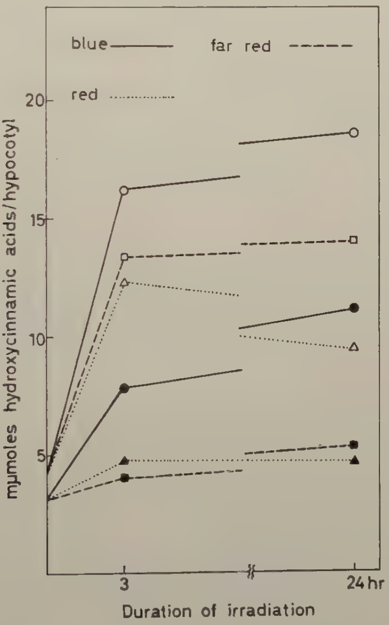

Fig. 3. Synthesis of hydroxycinnamic acids in the hypocotyls of intact seedlings (open symbols) and of decotyledonized seedlings (closed symbols) as a function of the duration of irradiation with blue, red and far-red light of 400 μW/cm² each.

The low responsivity to red light makes it difficult to study the occurrence of a red/far red antagonism. From the experiments with segments no direct evidence could be obtained that phytochrome participates in this process. Maintaining the segments on ice during the irradiation did not increase the results. According to HOPKINS and HILLMAN (1965) this technique prevents a rapid loss of phytochrome.

Effects of excision

In order to test in how far the differences in stimulation of phenol synthesis by small light doses between intact plants and segments are due to effects of excision the following experiment was performed. A box with at least 300 seedlings, having been picked for a uniform length, was irradiated for 10 min with blue (600 μW/cm^2) or red light (1200 μW/cm^2). Immediately after return to darkness, and after 1, 2, 3 and 6 hours respectively, segments were cut from the hypocotyls and transferred in duplicate lots of 30 segments each to petri dishes with 10 ml of the cinnamic acid, glucose solution. All samples remained in the precursor solution in darkness for 24 hours. For both light qualities it appeared that segments excised immediately after the light treatment showed a much lower capacity to convert cinnamic acid to p-coumaric acid than segments which remained part of the plant for at least one hour. No significant differences were observed between segments excised one hour after the light treatment and segments excised after six hours. The result of this experiment can be explained in different ways. For instance

1) A factor involved either in the enzyme induction or in the activation of the hydroxylase reaction moves from other parts of the plant to the part to be excised.
2) Excision introduces a factor which interferes with the enzyme induction.

An attempt to discriminate between these two possibilities and to evaluate the relative contribution of the effect of excision for the different spectral regions, was undertaken in the following experiment. From a box with three-days-old seedlings the cotyledons of 20 seedlings were covered with aluminium foil. From 20 plants the cotyledons and

TABLE 2

Influence of different covering and cutting treatments on the stimulation of the conversion of cinnamic acid into p-coumaric acid by blue, red and far-red light respectively. Numbers are mμmoles p-coumaric acid/hypocotyl segment accumulated during 24 hours in darkness

State of the seedlings during irradiation	Time between beginning of light treatment and excision (min)	Light treatment			
		10 min Blue 600 μW/cm^2	10 min Red 1200 μW/cm^2	30 min Far-red 600 μW/cm^2	Darkness
Hypocotyl segments		10.7	8.6	9.3	8.5
Intact seedlings	10	11.2	9.8		
Intact seedlings	120	13.2	11.4	13.0	
Cotyledons covered	120	11.0	10.1	10.8	
Cotyledons excised	120	10.6	9.7	10.3	
Cot. + pl. hook excised	120	10.0	8.4	10.3	

from another 20 plants cotyledons plus plumular hooks were excised. From other seedlings two lots of 20 hypocotyl segments were prepared and put in petri dishes with the cinnamic acid, glucose solution. One lot received together with the seedlings in the box the light treatment which consisted of 10 min of blue (600 μW/cm^2), 10 min of red (1200 μW/cm^2), or 30 min of far-red light (600 μW/cm^2) respectively. The other lot served as dark control. Immediately after the light treatment the aluminium foil was removed, and from 20 plants, of which both cotyledons and hypocotyls had been irradiated, segments were excised (except in the experiments with far red). From all other plants segments were cut two hours from the beginning of the irradiation. The accumulation of p-coumaric acid ester in the segments that were kept in the precursor solution in darkness for 24 hours is presented in Table 2. The data are averages of 9 to 12 experiments.

The results show:

1) Photo-stimulation of the hydroxylating capacity is much higher when the entire plant is irradiated instead of a segment, and the part to be excised remains in contact with the surrounding tissue for some time (about one hour) after the end of the (short) irradiation.
2) Covering or excision of the cotyledons lowers the capacity of the hypocotyl segments to convert cinnamic acid into p-coumaric acid.
3) The relative contribution of the excision effect on the photo-induction is higher in the case of irradiation with red or far-red light than with blue light.

4. Discussion

A generally accepted mechanism for hydroxycinnamic acid biosynthesis in higher plants is the shikimic acid pathway (Neish, 1964). However, in the gherkin seedlings the majority of the "proto-aromatic compounds" failed to stimulate the synthesis of p-coumaric acid. Stimulation was only obtained with L-phenylalanine and trans-cinnamic acid. The importance of L-phenylalanine as an intermediate in the formation of hydroxylated aromatic compounds has been established for a number of plants (Neish, 1964; Zenk, 1964; Zenk and Müller, 1964). It may be possible that at this stage of development of the gherkin seedling the entire shikimic acid pathway does not yet function and that the hydroxycinnamic acids and lignin are synthesized exclusively from phenylalanine originally stored in the seed.

Enzymes which catalyze the steps from phenylalanine to p-coumaric acid have been isolated. Koukol and Conn (1961) have purified phenylalanine deaminase from barley, while Nair and Vining (1965) have demonstrated the existence of a cinnamic acid hydroxylase in spinach leaves. They found that the unstable enzyme requires tetrahydrofolic acid and a reduced pyridine nucleotide to obtain maximum activity.

As already stated, the major product of the feeding experiments in gherkin hypocotyl segments is the monoglucose ester of p-coumaric acid. Working with potato tuber tissue LEVY and ZUCKER (1960) have obtained evidence that hydroxylation of cinnamic acid is preceded by esterification. With the gherkin hypocotyl segments no direct influence of externally supplied glucose on the conversion of cinnamic acid into p-coumaric acid glucose ester could be found. Although no strict evidence is available, we assume that the effect of light in our system is on the hydroxylase step.

Experiments with cycloheximide and chloramphenicol have demonstrated the involvement of *de novo* enzyme synthesis (ENGELSMA and MEIJER, 1965a; ENGELSMA, 1965). Whether this concerns hydroxylase itself or, for instance, one or more enzymes involved in the synthesis of a co-factor has not yet been established. Evidence of induction of enzyme synthesis in higher plants in response to light has also been obtained for the formation of chlorophyll in beans and maize (BOGORAD and JACOBSON, 1964), anthocyanin in mustard seedlings (MOHR and LANGE, 1965) and chlorogenic acid in potato tuber slices (ZUCKER, 1963).

Up to a limit of about 8 hours the increase in hydroxylase activity in hypocotyl segments is roughly linear with the duration of the irradiation in blue light. The rate increases with increasing light intensity until a saturation level is reached. The induction apparently depends on a continuous excitation of a pigment by the light. The mechanism leading from light perception to enzyme induction is still obscure but two recent findings may be relevant. WILLIAMS and NOVELLI (1964) have discovered that ribosomes from maize shoots acquire an enhanced capability of incorporating C^{14}-leucine into protein two hours after the plants have been transferred from darkness to the light. And CLARK *et al.* (1964) have found that on exposing Brassica pekinenses leaves to light, a rise in polyribosomes can be detected within 4 minutes, which, at least in part, appears to be associated with the synthesis of new RNA.

Our experiments provide some evidence that a mobile factor is involved which enhances the hydroxylase activity in the hypocotyls. In particular the effect of covering the cotyledons does not lend support to the idea that the low responsivity of the segments to red and far-red light is due to wound artefacts interfering with the process of enzyme induction. In 8 out of 10 experiments with intact plants we found that the accumulation of hydroxycinnamic acids in the hypocotyls in response to a small dose of red light (3.5 kerg/cm^2) was lower when only the hypocotyls were irradiated (unpublished results). It should be noted, however, that covering the cotyledons may have a certain traumatic effect.

Whether the transported factor from the cotyledons acts on the level of enzyme induction or enzyme action is still unknown. Its relative contribution to the increase in hydroxylase activity in the hypocotyls seems higher in the case of irradiation with red and far-red light than with blue light. If this is taken into account we obtain a good correlation between hydroxylase activity and accumulation of phenols under different light conditions. We do not yet know whether the enzyme activity in the preceding step, deamination of phenylalanine, is already so high that it never becomes rate-limiting, or that the phenylalanine deaminase activity is stimulated to an extent comparable with the stimulation of cinnamic acid hydroxylase activity.

The induction of hydroxylase activity seems to be an important link in the regulatory mechanism for lignification and hypocotyl elongation (ENGELSMA and MEIJER, 1965b). Influences of oxygen tension and of oxidizing and reducing agents on these phenomena (SIEGEL and PORTO, 1961) may be at least partly due to their effects on the hydroxylating enzyme. We found that supplying ascorbic acid to the segments has no effect on the induction of cinnamic acid hydroxylase but enhances its activity.

The accumulation of hydroxycinnamic acids in the hypocotyls of continuously irradiated seedlings becomes more or less saturated within 24 hours, as has been shown previously (ENGELSMA and MEIJER, 1965a, Fig. 6). Experiments with hypocotyl segments from such plants, irradiated for 24 hours, showed that a further accumulation occurs when they are supplied with phenylalanine or cinnamic acid. When experiments as presented in Fig. 2B of this paper are carried out over a period of 48 hours the amount of p-coumaric acid that accumulates is about 160 % of the amount obtained in the 24-hour experiments. This indicates that under natural conditions the hydroxylase activity does not become blocked but that phenol-producing and consuming reactions attain an equilibrium.

It is still far from understood which pigment systems are involved in photomorphogenesis and through which mechanism the only photoreceptor so far established, phytochrome, causes the observed biochemical and morphological changes. The responsivity to blue light of the process studied here is much higher than that to the other spectral regions, the difference being greater than for phenol synthesis and inhibition of hypocotyl elongation of intact seedlings. This would be difficult to understand on the basis of phytochrome, which has its main absorbance in the red, far-red region. Preliminary experiments on the determination of an action spectrum show that the highest sensitivity lies in the 430–470 mμ region where neither of the two forms of phytochrome has an absorption maximum (BUTLER, HENDRICKS and SIEGELMAN, 1965).

Experiments with a very sensitive growth meter have revealed that the lag for inhibition of hypocotyl elongation in blue light is even shorter than reported previously (ENGELSMA and MEIJER, 1965b), being less than one minute (Meijer, to be published). The recording of the growth rate as a function of time of a dark-grown seedling transferred to blue light differs characteristically from those obtained on exposing a dark-grown seedling to red or far-red light. This indicates that growth inhibition in blue light is also at least partly due to a process not mediated by phytochrome. The above does not imply that phenol synthesis and rapid growth inhibition in response to blue light are necessarily mediated by the same pigment system.

Returning to the phenol synthesis in the hypocotyls of intact plants, we find that the effects of red as well as far-red light, in contrast to blue light, are mediated to a predominant extent by the cotyledons. This situation is not in disagreement with the hypothesis that both the effects of red and far-red light are mediated by the same photoreceptor, phytochrome (Butler *et al.*, 1963; Hartmann, personal communication, see also Bertsch and Mohr, 1965). To account for the energy dependence observed for far-red irradiations (Engelsma and Meijer, 1965a, Fig. 6) it seems necessary to assume, however, that the process not only depends on the ratio of the two forms of phytochrome but also on a continuous perception of the light by this or another pigment as argued before for blue light.

The sensitivity of the different excised parts of the hypocotyl to red and far-red light for the stimulation of phenol synthesis shows a correlation with the distribution of chlorophyll accumulating in response to light. Similar conclusions have been reached by Björn and Virgin (1958) for the influence of red light on the growth of pea seedlings. They state that the distribution of the areas giving the strongest response to red irradiation seems to agree with the sites for the formation of the green and yellow pigments of the plant. Whether, as these authors ask, the structural relationship between the light-absorbing groups of phytochrome and chlorophyll, both being pyrrole pigments, has any bearing on this, is still an open question.

A correlation between the intensity of the yellow colour of the etiolated hypocotyl and the sensitivity to blue light for the induction of hydroxylase activity can also be observed. Yellow pigments in the etiolated hypocotyl and chlorophyll in the light-treated hypocotyl show a similar distribution pattern. The assumptions that the effect of blue light is mediated by the yellow pigment(s), probably carotenoid(s), and those of red and far-red light by phytochrome, and possibly other pyrrole pigments, would explain the results presented in Fig. 1.

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Note added in proof. Since the preparation of this manuscript it has been found that light stimulates *de novo* synthesis of the enzyme fenytalanine deaminase in the gherkin hypocotyl to a similar extent as cinnamic acid hydroxylase.

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CALCIUM CONTENT OF FRUITS AND STORAGE TISSUES IN RELATION TO THE MODE OF WATER SUPPLY

L. K. WIERSUM

(*Institute for Soil Fertility, Groningen, the Netherlands*)

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Abstract

Experiments were performed to elucidate the process of uneven distribution of Ca between different parts of the plant. The Ca-contents of fruits and storage tissues are usually extremely low, and as a result local disorders may occur.

The primary distribution of ^{45}Ca was found to be closely linked to the distribution of water along the xylem vessels. During the period of fast growth no or hardly any water and ^{45}Ca entered tomato fruits, apples, potatoes or seeds of the broad bean. This phenomenon is explained by accepting the existence of a mass flow transport in the phloem. This mass flow can supply the necessary water along with most other nutrients, but does not carry any worthwhile amount of Ca.

In a further series of experiments it is demonstrated that conditions conducive to predominance of the sieve tube transport result in a lowered Ca-content of tomato fruits and increased blossom-end rot. Conditions favouring an auxilliary supply of water via the woodvessels reduce the disease incidence and the K/Ca ratio of the fruits.

1. Introduction

In plants certain physiological disorders can occur which are correlated with local insufficiency of a special element. In tomatoes the incidence of blossom-end rot increases as the calcium content of fruit diminishes and the K/Ca ratio rises (Evans and Troxler, 1953; Geraldson, 1957; Lyon *et al.*, 1942; Maynard *et al.*, 1957). Bitter pit of apples also shows a relationship to a low calcium content of the fruit (Askew *et al.*, 1959, 1960; Baxter, 1962; Bouhier de l'Ecluse, 1962; Kidson *et al.*, 1963; Martin *et al.*, 1964; Van Schreven *et al.*, 1962, 1964). In peas the occurrence of marsh spot is related to a manganese deficiency, which can hardly be cured by spraying the leaves only with this element (Henkens and Jongman, 1965). Internal tipburn of cabbage is also correlated with a local low Ca-content (Maynard *et al.*, 1965).

One of the most striking characteristics of a number of these disorders is that the calcium content of the organs, which may be affected, is always very low in comparison to that in the sprout. If the general supply status of the plant diminishes the content in these tissues becomes so very low as to result in a mineral unbalance.

Data on blossom-end rot published by Geraldson (1957) show that the tomato fruit contains only as much as 0.10–0.24 % Ca, while the leaves have a level of 0.84–4.14 % on dry weight. Data given by Ward (1964) confirm this very uneven distribution of calcium. According to Garman (Bouhier de l'Ecluse, 1963) the calcium content of apples is only 1/20–1/80 part of that in the leaves. This low calcium content of the fruit is the result of a very slow influx of this element into the growing apple, especially in comparison to the much better supply with assimilates, N, P and K (Askew *et al.*, 1959, 1960). Potatoes also show a low calcium content compared with the sprout (Hagemann, 1964) and extremes can be linked with a poor keeping quality of seed potatoes in storage. Distribution of radioactive strontium, which behaves similar to calcium, in the potato shows the same pattern (Mecklenburg and Tukey, 1963). Investigations by Läuchli (1962) on the distribution of strontium administered to pea plants also demonstrate that the relative content of the seeds is only 1/25 of that of the leaves and stems and 1/12 of that of the carpels.

The above mentioned facts demonstrate that calcium is not evenly distributed over the plant. This might be related to a restricted supply, a conclusion which was already drawn by Mason and Maskell (1934) in regard to cotton seed. Thus the possibilities of transport will have to be considered.

Transport of calcium from cell to cell in the symplasm is noticeably slow (Arisz) and as usually larger distances are involved, this pathway can be left out of consideration. Two modes of long distance transport exist in the plant: either along with water in the woodvessels or by means of movement in the sieve-tubes.

The primary means of distribution of root-absorbed calcium will be in the transpiration current or otherwise induced water transport in the xylem. The calcium carried along this way undergoes continuous loss, exchange or gain (Bell, 1963; Biddulph *et al.*, 1961) with the surrounding tissues. So, although calcium transport entirely depends on water movement in these vessels the amount transported does not have to be highly correlated to the amount of water arriving at a certain destination.

For several ions the phloem forms a second pathway of transport. Most evidence related to calcium points to the fact, that this ion is more or less immobile in the sieve tubes (Biddulph *et al.*, 1958; Crafts, 1961; Mason and Maskell, 1934; Norton and Wittwer, 1963; Ziegler, 1962). In the few cases where redistribution of calcium has been demonstrated it often does not seem necessary to suppose that a phloem transport is involved (Bukovac *et al.*, 1956; Ferrell and Johnson, 1956; Vlasyuk and Grodzinskii, 1960, 1965). If calcium can escape into the apoplast (mainly the cell walls and the xylem), transport along with water following hydrostatic gradients is a possibility (Crafts, 1956). The very slight transport of calcium in the sieve tubes is easily understood when their very low calcium content is taken into account. Analysis of exuding phloem-sap by Tammes and Van Die (1964) show a calcium content of 0.014 mg/ml and a K/Ca ratio of 120.

In regard to the fact that calcium supply is linked to water supply over the xylem it seemed necessary to investigate the water movement to the affected organs. Former research on peanuts (Wiersum, 1951) had already lead to an explanation of the missing calcium supply of the pods of Arachis.

2. Experiments on water and calcium transport in the xylem

2.1. *Experiments with tomatoes*

Tomato-plants (var. Moneymaker) were grown till they carried 3–4 trusses. At this stage the lowest truss would already carry some nearly full grown fruits. The plants were taken out of the pots and the roots washed free of soil. They were then transferred to a half strength nutrient solution.

For the experiments a glass vessel was filled with 600 ml of this dilute nutrient solution to which about 10 μC ^{45}Ca had been added. Some dye in the form of Light Green was added to obtain a blueish solution. The plants were then put into this solution after having cut away most of the roots. This was done to allow free entrance of the dye into the xylem, which was to be used as a visual tracer for water-transport.

The experiments lasted 3–4 days and during that time the plants were in the laboratory under additional artificial lighting. At the end of the experiment different parts of the plants were inspected for presence of blue colouration. Fruits were cut lengthwise into slices 2–3 mm thick near the centre. The parts to be investigated further were cut off the plant and then dried at 105° C. Sometimes a provisional radioactivity measurement was performed on the fresh material.

Distribution of ^{45}Ca was investigated by means of autoradiography. The exposures on the Kodak No Screen Medical X-ray film usually lasted about 14 days. Longer exposures did not show activity in parts not already showing up in the ordinary exposure time.

The distribution of Light Green in the plants was usually as follows. All leaves showed a blue colour along the veins and sometimes even in the parenchymatous tissues. The intensity was variable over the different leaves. Often the younger leaves at the top showed the best colouration. The blue colour could also be detected in the stems of the trusses and even in the pedicels and calyx of the fruits. Inspection of the fruits, however, showed an abrupt ending of the colouration at the point where the pedicel is attached. Only in 1 or 2 cases could some slight trace of blue be detected in one of the many larger veins in the fruit wall.

The pattern of distribution of ^{45}Ca correlates with the occurrence of Light Green. Leaves, stems, young flowers, pedicels and calyx could all contain this ion. As far as the fruits are concerned blackening of the film was only found at the extreme base of young, small fruits, while never any ^{45}Ca could be recorded in medium or larger sized fruits. In Plate I the result of an experiment is depicted.

In one experiment water consumption by the plant and growth of the fruits was measured. The plant with 15 expanded leaves absorbed about 240 ml solution. A single leaflet may thus average a waterloss of a bit more than 2 ml. The increase in size of some half grown tomatoes was even slightly more. But none the less they do not receive any colouring substance or ^{45}Ca.

2.2. *Experiment with apple*

A few twigs, carrying young fruits, were cut from an old Jonathan tree. In the laboratory a fresh cut was made and the twigs placed on the same dilute nutrient solution with Light Green and ^{45}Ca added. Within a few hours the first traces of colour could be detected in the leaves.

After 2 days the twigs were removed and inspected. The results are given in Table 1 and Plate II.

TABLE 1

Distribution of Light Green and ^{45}Ca in apple twigs

twig	colour	^{45}Ca
I leaves	strong colour	high content over whole lamina
2 cm fruit	some near base	same pattern of distribution
3 cm fruit	base and veins along cavity	
II leaves	well coloured	high content
1½ cm fruit	some colour	some Ca in base and decreasing towards tip
1½ cm fruit	some colour	
4 cm fruit	colour in base, along cavity and tip	Ca in stem and main central veins

Again we find that the leaves obtain a large amount of Light Green and ^{45}Ca, while the amount entering the fruits is small in comparison.

2.3. *Experiments with potatoes*

The plants used in the experiment were grown in the glasshouse in plastic pails, the bottom of which had been replaced by a wire screen. The lower part of the pail was filled with garden soil and on top of a layer of nylon gauze sand was filled in. The pails were placed on top of vessels containing a dilute nutrient solution. In this setup part of the root system would grow from the soil into the solution. Growth of stolons and young tubers was restricted to the top layer of sand.

For the experiments the protruding root system was partly cut off and the plants in the pails were placed on top of a vessel containing a dilute nutrient solution + Light Green and 10 μC^{45}Ca per 600 ml. Usually part of the stems were cut off to remove excess foliage. A comparison was always made between plants with the stolons and young tubers buried in the sand and plants where the sand had been removed to expose these organs to the air.

The period of uptake varied from 2–5 days.

Inspection of the plants at the end of the experiment usually showed a light colouring of the leaves, mainly in the veins, and blue coloured xylem in the stems. As far as the stolons and young tubers are concerned there was generally a clear blue colour visible in the stolons exposed to the air. Cuts through the tubers exposed the blue colours in the vessels and sometimes the eyes were coloured. If the stolons and the tubers had remained buried in the sand an exceptional blue colouration would be noticeable if the sand had been very dry. In well moistened sand these parts remained white.

The results of the radioautographs demonstrated a corresponding distribution of ^{45}Ca. Colouring of the leaves and their filmprints showed a good correlation. Stolons exposed to the air gave the strongest blackening on the films. Exposed tubers were found to contain ^{45}Ca in reasonable amounts, mainly at the base and in the tissues between the circle of veins and the surface. Buried stolons and young tubers were generally devoid of any ^{45}Ca.

We may conclude that under normal circumstances the water taken in by the roots is nearly all transported to the aboveground parts of the plant, carrying along the ^{45}Ca and the dissolved Light Green. Only if the transpiration of the stolons and young tubers is raised by exposure to air does a worthwhile amount of the absorbed solution enter these organs. An example of the results is depicted in Plate III.

2.4. *Experiment with broad bean*

Medium sized plants grown in pots were taken into the laboratory and their roots washed free of soil. All smaller roots were cut off and the plants were placed with their root stumps immersed in a dilute nutrient solution + Light Green and ^{45}Ca.

At the end of a 2–4 days absorption period the plants were inspected, samples removed and dried before being autoradiographed.

Inspection showed that the blue colour could be clearly seen in all plant parts: stems, leaves, flowers, young fruits and even in full grown fruits, mainly in base and tip. These large pods were carefully cut lengthwise through the main veins for further examination. The blue colouring could be traced all along the cut xylemvessels of the main carpel veins. There was, however, an abrupt ending of the colouration at the point where xylem vessels branched off to the seeds. Nowhere in the connecting strands or in the seeds, either small or large, could any colour be detected.

The results of the autoradiographs as given in Plate IV show exactly the same distribution for ^{45}Ca. This ion can be found in all parts of the plant and is even present in the pods to a fair amount. None, however, was ever traced in the sliced seeds.

For this plant we may conclude that the flow of water over the xylem to the seeds, by which means the main supply of Ca must occur, is restricted. All other parts are well supplied.

2.5. *Discussion*

All previously described experiments demonstrate the fact that certain plant parts, which are known to be relatively low in Ca-content, show a restricted or wholly lacking flow of water through the xylem to these organs. De Kock (1964) also suggests the uneven calcium distribution as being linked to a large water supply for transpiration or a large supply of assimilates. This restricted xylem water influx does not necessarily hold for their whole period of growth. The water supply by means of the woodvessels seems to be most severely restricted when the affected parts are in a stage of fast growth. When these parts, such as tomato fruits are still very small there still seems to be an influx of water and of ^{45}Ca. Corresponding behaviour has been noticed for buds of pear trees (GOUNY and HUGUET, 1964).

The pattern of distribution of ^{45}Ca more or less corresponds to the flow of water in the wood-vessels as indicated by the colouring. The main point is, that lack of calcium supply is always linked to an inhibited flow of water in the xylem to these parts. If the flow is only restricted – as is the case in young apples – the influx of Ca decreases accordingly.

Confronted with the fact that all plant parts investigated are organs, which show a large increase in size and thus surely will need a large supply of water this discrepancy needs explaining.

For an explanation reference can be made to a conception at which MÜNCH (1932) arrived in his work on transport in the phloem. The hypothesis of transport in the phloem occurring by means of mass flow (CRAFTS, 1961; ZIEGLER, 1963) implies that a large amount of water in which the assimilates are dissolved moves towards the sinks where the substances are laid down (CRAFTS and CURRIER, 1963). If the total consumption of water in these parts – growth plus transpiration – is not too high the amount of water arriving by means of the phloem could even be in excess of the needs. Excess water is then supposed to flow back in the xylem (MÜNCH, 1932). Recently, results obtained by ZIEGLER (1963) give evidence supporting this interpretation.

3. EXPERIMENTS TO INFLUENCE CALCIUM TRANSPORT BY MEANS OF RETARDED OR ENHANCED WATER TRANSPORT IN THE XYLEM

Taking the explanation given above for granted the possibility of shifting the balance between waterconsumption and supply of water over the phloem was investigated. The idea was that restricted transpiration of the fruits or faster growth of these parts should lead to a dominance of water supply over the sieve tubes. Contrary, retarded growth of the fruits should lead to a relative increase of transpiration in the total waterconsumption, which might bring about the necessity of additional water supply over the xylem. This additional influx of water should result in a better calcium supply.

3.1. *Experiments with tomatoes*

An experiment based on the considerations given above was performed in which it was attempted to modify the incidence of blossom-end rot in tomato-fruits by appropriate treatments.

Five sets of tomatoes were grown with intervals of three weeks. Young plants of the variety Renova were planted in buckets filled with a sand-peat mull substrate. Fertilizing was done in a manner to obtain susceptibility to blossom-end rot. The plants were detopped after formation of the sixth truss and each truss was allowed to carry only five fruits.

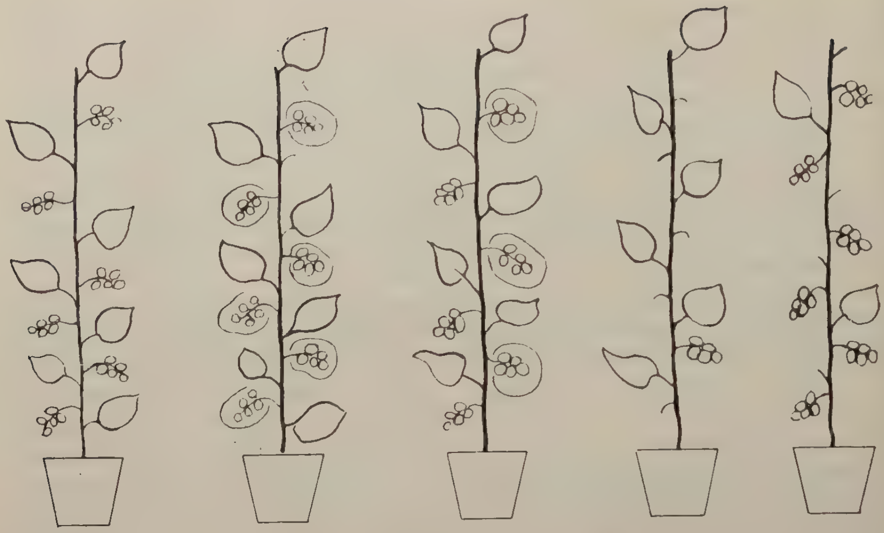


Fig. 1
Schematic drawing of the five treatments imposed on the tomato plants: control, bagged, alternatingly bagged, only 1 truss left, defoliated.

The following treatments were applied (Fig. 1)

1 control, normal with 6 trusses of 5 fruits
2 restricted transpiration, all 6 trusses enclosed in translucent plastic bags
3 alternating, free and enclosed trusses alternating
4 enhanced growth, only 1 truss remains on the plant by removing the 5 others
5 restricted growth, only 1/3 of the foliage left on the plant carrying 6 trusses

Growth of the fruits was recorded by weekly measurement of the diameters.

The data in Table 2 clearly show that the treatments imposed have indeed influenced the growth rate. Transpiration must have been affected as water condensed in the bags, so the atmosphere around the fruits must have been near to saturation.

The effect of the treatments on the fruits is given in Table 3 and

Table 2
Average increase of fruit diameter in mm/day of identical trusses in each of the 5 series

enhanced growth 1 truss	normal control	retarded growth 1/3 leaf
0.98	0.96	0.95
1.26	1.15	1.13
1.54	1.14	1.01
1.12	0.99	0.93
1.09	1.08	1.00
		$P = 0.0008$

TABLE 3

Percentage blossom-end rot in relation to growth rate and transpiration

series	bagged	1 truss	control	1/3 leaf
1	20	0	20 0	0
2	100	100	0	0
3	25 80	80	0	0
4	60	20	0 20	0
5	0	0	0	0
average	47.5	40	6.7	0
				$P < 0.1$

TABLE 4

K/Ca ratio in fruits of identical trusses in different treatments

series	bagged	1 truss	control	1/3 leaf
1	16.0	12.7	14.8 13.3	7.7
2	21.9	20.5	15.1 15.4	11.7
3	15.4 15.6	14.1	11.2	9.7
average	17.2	15.8	14.0	9.7
				$P = 0.017$

in Table 4 the data on chemical constitution are summarized. The results clearly form a confirmation of what was expected. The incidence of blossom-end rot is the highest under conditions of reduced transpiration. Faster growth also gives a high percentage affected fruits, while restricted growth rate results in a low disease incidence. The K/Ca ratio correlates with the percentage diseased fruit. Reduced transpiration does indeed lower the Ca-content, while retarded growth results in the highest Ca-percentage. Enhanced growth rate mainly results in a high K-content, which may be the result of increased influx via the phloem along with the assimilates.

A Ca-content less than 0.08 % on dry matter always gives rise to blossom-end rot. If the calcium content rises above 0.12 % all fruits are healthy. These data are well in accord with those given by GERALDSON (1957).

The conclusion is that the results lend support to the idea that the tomato fruit obtains its water by means of two different pathways, the most important of which is the phloem. The Ca-supply is related to the amount of additional water drawn towards the fruit by means of the xylem.

This interpretation gives us an understanding of the observations that the incidence of blossom-end rot in horticultural practice is related to an insufficient water supply under conditions of high transpiration (EVANS and TROXLER, 1953; HÅRDH, 1957), low Ca-

and high K-content of the soil (Evans and Troxler, 1953) and fast growth as may be induced by a high N-fertilization (Hårdh, 1957; De Vries, 1958).

3.2. *Experiment with apple*

The experiment was performed on an old, rather poor, Jonathan tree. Two treatments were applied. On the south side of the tree many smaller twigs were pruned and the remaining twigs partly defoliated. The purpose was to retard development of the fruits occurring on them. At the opposite side of the tree pruning was also carried out and the remaining very young fruits along with some leaves were enclosed in translucent plastic bags. The remaining fruits on the tree were taken as controls. At ripeness the fruits remained small and were often somewhat misshapen as a result of insect damage.

After harvesting them the fruits were cut into pieces and dried. Later they were ground to a coarse powder, ashed and analysed for Ca and K.

The poor quality of the material and the restricted number of analyses did not give significant differences. A very slight indication was obtained that bagged apples might contain a lower Ca- content, while the K-content remains unaltered. This could mean a corroboration of the results obtained on tomatoes.

That the imposed treatments can have the expected effects is already to be found in the literature. Boulay and Leblond (1963) notice a higher incidence of bitter pit of fruits grown in bags. Bouhier de l'Ecluse cites Krause that defoliation before plucking diminishes bitter pit (1962).

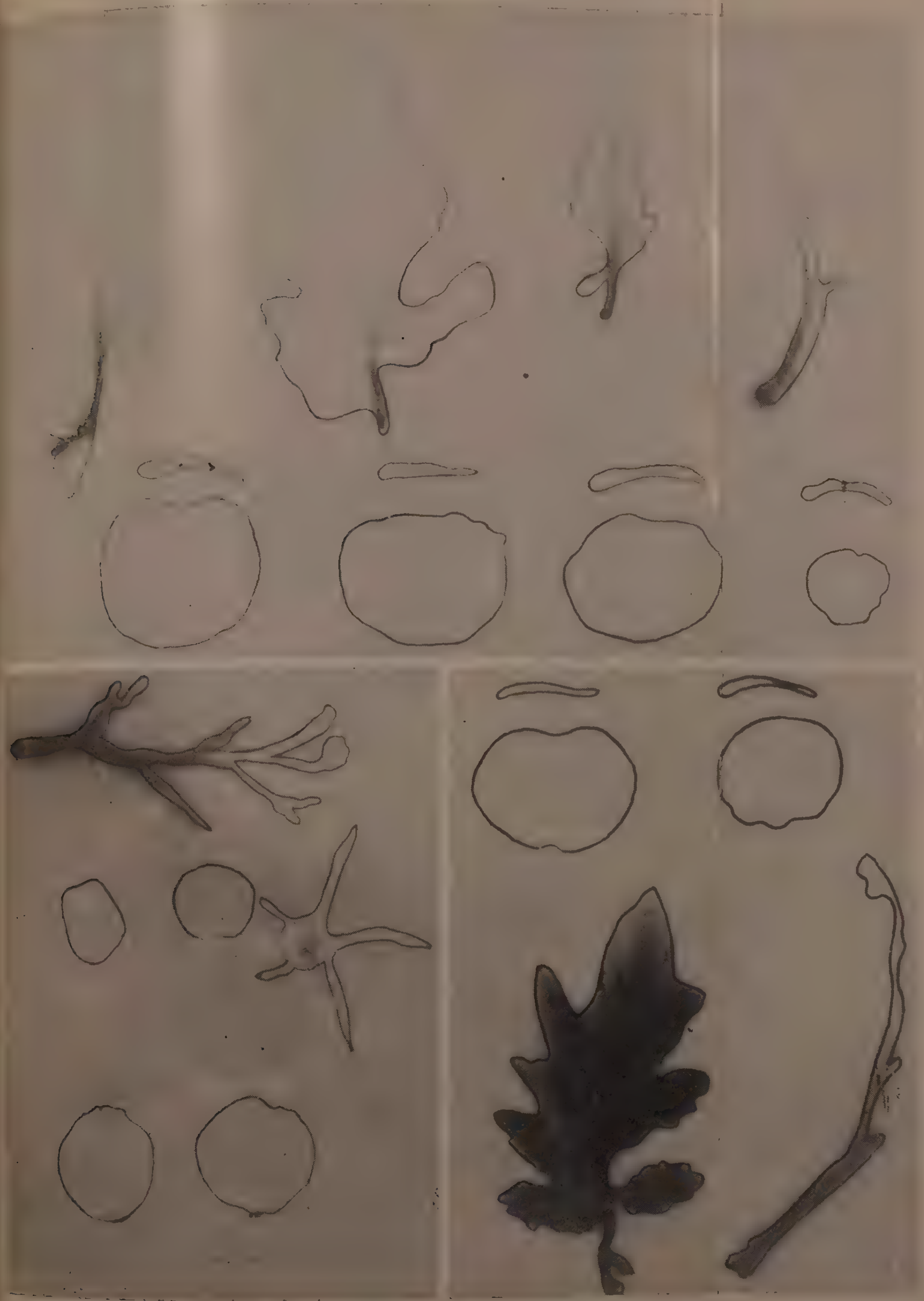
The validity of the supposition that the growing apple fruit in its stage of fast growth receives little water over the xylem is supported by the fact that the influx of N, P, and K follows the gain in weight and Ca-influx is extremely slow (Askew *et al.*, 1959/60, 1960). The same contrast in behaviour regarding influx in the cherry seed for ^{90}Sr and ^{137}Cs has been noticed by Eynard (1963). In this stage the Ca-content of the apple undergoes a relative dilution.

That fruits growing on the sun-exposed side of the tree have better keeping qualities in regard to bitter pit than those on the more shaded side, can possibly be explained by envisaging a higher transpiration. This difference has been noticed in practical experience with certain varieties in South Africa (de Haan).

3.3. *Discussion*

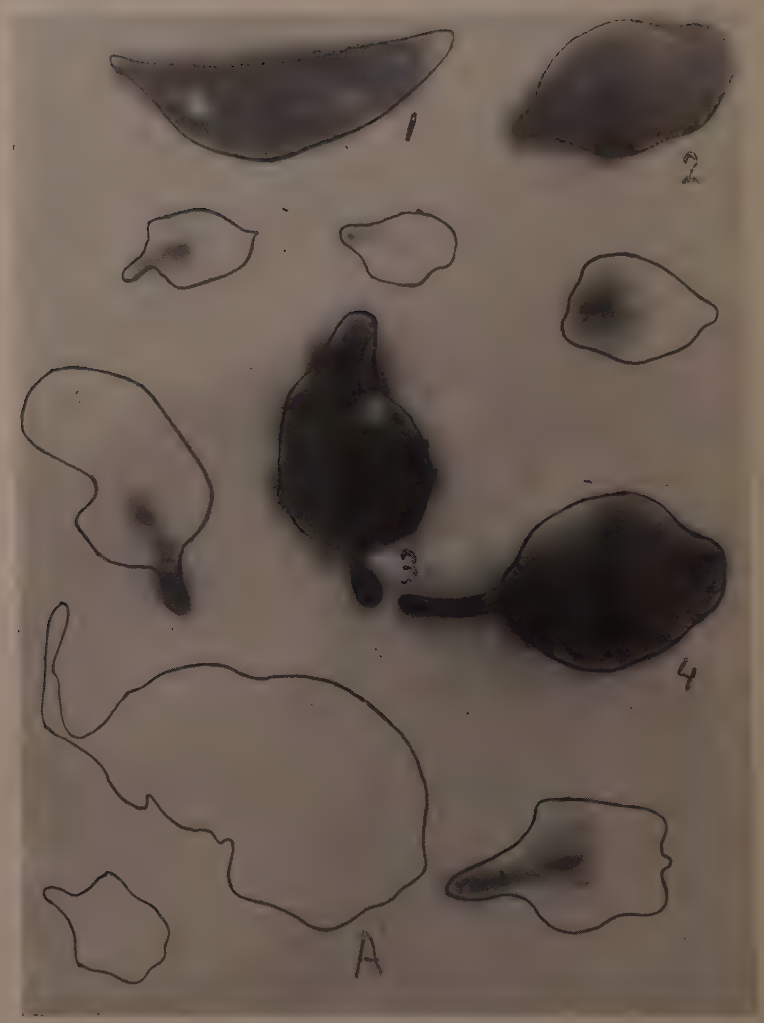
The results of these experiments, which are based on the supposition that there are two modes of water supply to these fruits, support the idea that the balance can be shifted. The Ca-supply is correlated with the amount of water entering by means of the xylem, which during certain periods is very small. So this investigation indirectly demonstrates the validity of the conception that transport in the phloem occurs by means of mass flow.

L. K. WIERSUM: *Calcium content of fruits and storage tissues in relation to the mode of water supply*



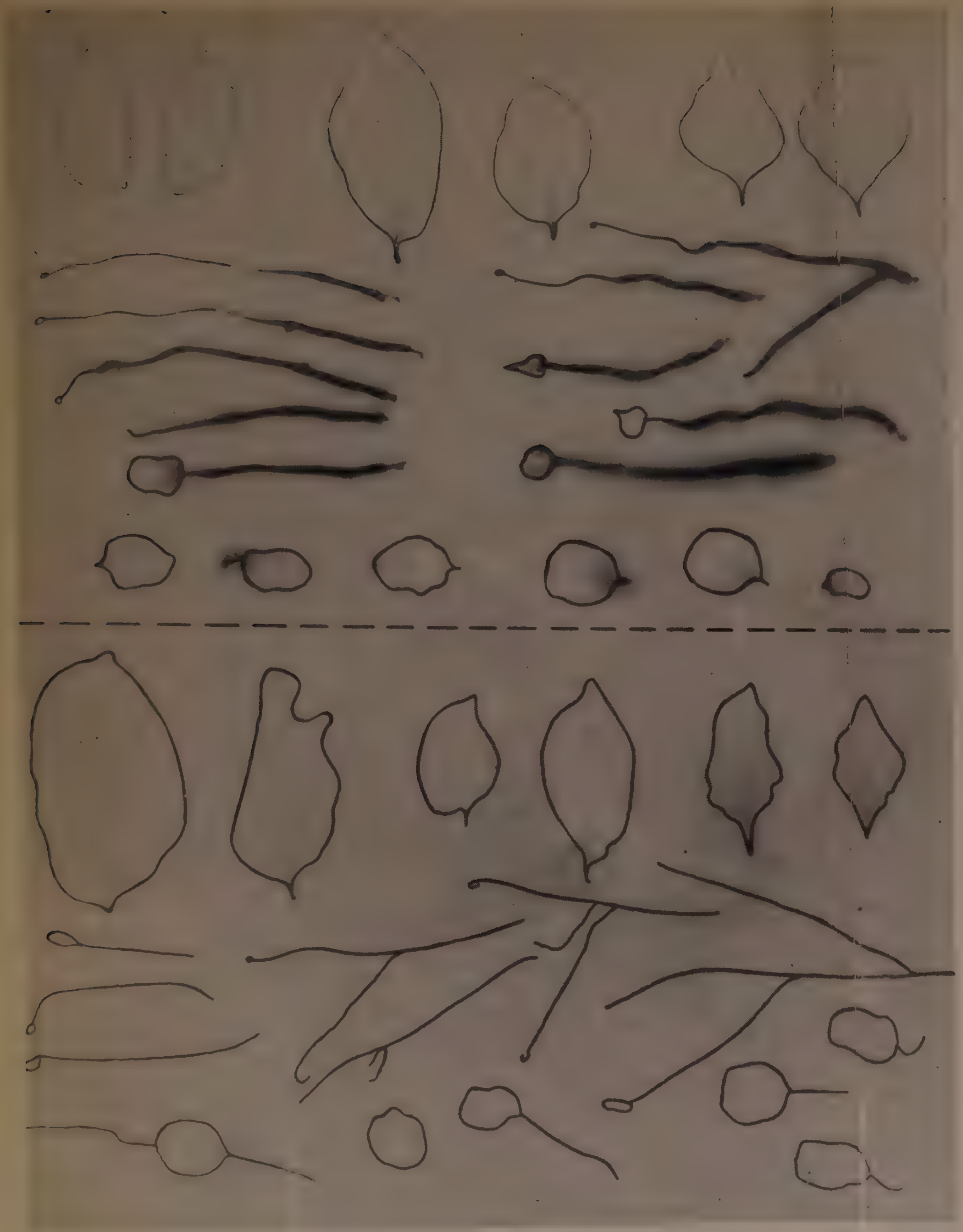
Autoradiographs of the primary distribution of ^{45}Ca in the tomato plant. Ca detectable in all plant parts (leaves, young truss, truss stem and calyx base) except in the fruit.

PLATE I



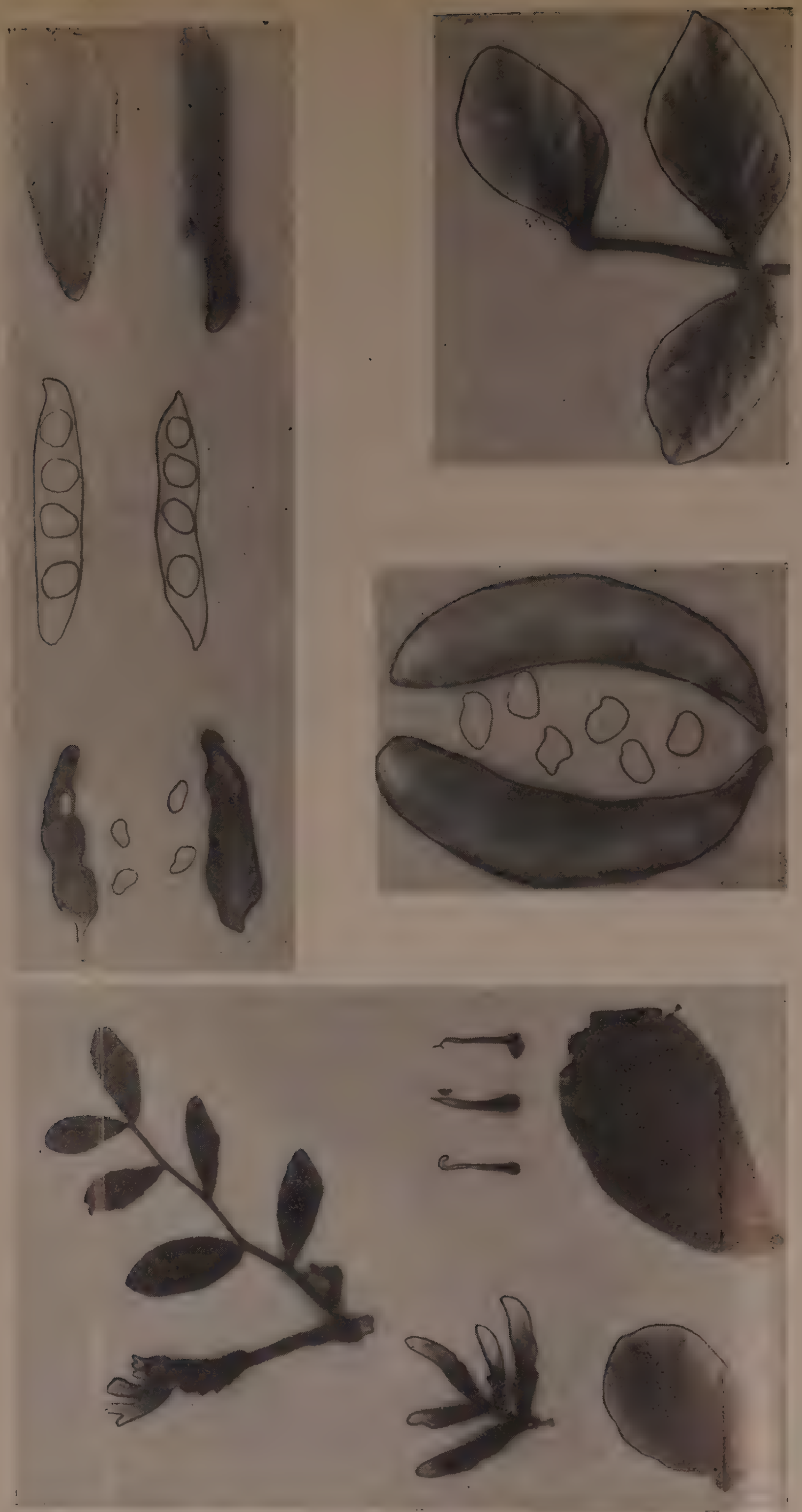
Autoradiographs of ^{45}Ca absorbed by cut stems in the apple. Ca detectable in leaves (1, 2, 3, 4) and in the base of young fruits, none in larger fruit (A).

PLATE II



Autoradiographs of ^{45}Ca distribution in the potato. Upper part: plant with stolons and young tubers exposed to air shows Ca both in leaves, stolons and tubers. Lower part: plant with buried stolons and young tubers only has ^{45}Ca in the leaves.

PLATE III



Distribution of ^{45}Ca in the broad bean. Ca is detectable in all plant parts except the seeds.

PLATE IV

This balance between the two modes of water supply varies during development. In our own experiments we found a good supply of water and ^{45}Ca entering flowers and very young fruits by means of the woodvessels. In the stage of expansive growth this supply is more or less eliminated. The situation can again change in full grown fruits. This can be deducted from the data given by ASKEW *et al.* (1959, 1960) on the mineral content of the apple during growth. The young apple starts with a more or less normal Ca-content. Then comes a period of extremely low influx and a strong dilution. Only when the flux of assimilates, N, P, and K comes to an end at ripeness, does the Ca-content rise again. This would mean that with the diminishing supply of organic materials also the water influx over the phloem decreases and that xylem influx bringing in Ca-containing water partly takes over.

A number of experiences in apple growing can now be well understood. Severe thinning of apples, resulting in fast growth and large sized fruits, favours susceptibility to bitter pit and other storage disorders (SHARPLES, 1964). Large size fruits are in general more susceptible to bitter pit (BEYERS, 1962; VAN SCHREVEN *et al.*, 1962). Late plucking usually diminishes the incidence of bitter pit in storage. High water consumption by the leaves and slow supply from the soil enhances the incidence of bitter pit (BEYERS, 1962, n.n. 1964).

4. GENERAL REMARKS

From the results of these experiments the conclusion could be drawn that especially in their period of fast growth the investigated storage organs receive no or hardly any water at all by means of the xylem. Thus the most obvious means of Ca-supply is more or less eliminated.

The increase in volume and dry matter of these parts in the same period requires an influx of both water and assimilates along with mineral substances. The most obvious explanation is that these are supplied simultaneously by means of a mass flow, occurring in the phloem. Taking into account the extremely low Ca-content in the sieve tubes (TAMMES and VAN DIE, 1964; ZIEGLER, 1962) their ineffectiveness in Ca-transport is readily understood.

Although many investigators (BIDDULPH *et al.*, 1958; CRAFTS, 1961; ZIEGLER, 1962) have demonstrated the immobility of calcium in the phloem, there still remain some reports on redistribution of calcium in the plant, where previously absorbed calcium is shifted from one site to another. It seems likely that much of this evidence (BUKOVAC *et al.*, 1956; FERRELL and JOHNSON, 1956; KESSLER and MOSZICKI, 1958; MOSOLOV *et al.*, 1957; PETROV-SPIRIDONOV, 1964; ROBERTSON, 1963; VLASYUK and GRODZINSKII, 1960, 1965) can be explained by release of calcium into the woodvessels and displacement along the xylem following gradients of uneven waterstress (BIDDULPH *et al.*, 1959). A confirmation of this explanation was obtained in one of a few auxilliary experiments. ^{45}Ca applied to an immersed leaf could be detected in a nearby leaf exposed to a dry atmosphere. The plants were kept on a restricted water supply during the experiment to enhance the opportunity of inducing abnormal water movements.

Only under abnormal conditions, if the tissue is flooded with free calcium, does it seem to enter the phloem and to be transported by this means (ABUTALYBOV and DZHANGIROVA, 1961; MILLIKAN and HANGER, 1965).

SUMMARY

As a number of disorders in fruits and storage tissues is related to an insufficient Ca-content the mode of transport of this element was investigated. This mode of transport should also be able to explain the general very low Ca-content of these parts in comparison to leaf and stem tissues.

In a series of experiments with tomatoes, apples, potatoes and broad beans it could be shown that the distribution of ^{45}Ca follows the same pattern as that of the dye Light Green, which is carried along in the transpiration stream. During the period of fast growth neither dye nor ^{45}Ca enters the fruit, seed or the tuber.

This behaviour could be explained by accepting the occurrence of massflow in the sieve tubes supplying these parts with assimilates, water and other minerals, as the phloem-sap is extremely poor in Ca.

This explanation was further tested in experiments in which it was tried to shift the existing balance between the two modes of water supply. Restricted transpiration of the tomato-fruits, which eliminates accessory entrance of water via the xylem, indeed resulted in a still lower Ca-content and a higher incidence of blossom-end rot. Enclosing apples in plastic bags resulted in the same phenomenon. Reducing the water supply by means of the phloem by restricting growth rate resulted in a higher Ca-content, which is explained by accepting an accessory influx of water via the xylem.

The interpretation as given can explain a number of practical observations on the occurrence of blossom-end rot in tomatoes and bitter pit in apples.

In discussing the results it is pointed out that much evidence on redistribution of Ca may be explained by release into the xylem and translocation along with water in the woodvessels.

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TRANSPORT, IMMOBILIZATION AND LOCALIZATION OF NAPHTHYLACETIC ACID-1-^{14}C IN COLEUS EXPLANTS

H. VEEN

(*Centre for Plant Physiological Research, Wageningen, The Netherlands*)

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Summary

The transport and metabolism of naphthylacetic acid -1-^{14}C in explants of *Coleus* was studied by means of the liquid scintillation counting technique in combination with thin layer chromatography.

Microautoradiography was used to study the intracellular localization of the auxin.

The gross radioactivity in the tissue is mainly fixed just below the donor block. In this part of the explant the radioactivity is present in the cytoplasm next to the cell wall. Although all the radioactivity in the receiver block represents the auxin itself, tissue extracts showed an intense metabolic turnover of the auxin. A study was made of the time-dependency of the production of several compounds and the ratio between the compounds in extracts of different parts of the explant. Finally, the chemical identity of the substances is discussed.

Introduction

The growth substances known to control the vegetative growth of a wide variety of higher plants generally have to be translocated from their site of production to their site of action. The importance of auxin translocation is obvious in such phenomena as apical dominance and abscission.

Studies on abscission have been carried out either with whole plants, or explants (plants: Vendrig, 1959; Jacobs and co-workers, 1964; explants: Addicott and co-workers, 1949; Leopold and co-workers, 1964; Gardner and Cooper, 1943; Luckwill, 1956; Gorter, 1957 and 1964). Explants of bean and of *Coleus* have been most widely used. Those of *Coleus* are particularly well suited for studying the relationship between the abscission of the petioles and the transport of auxin.

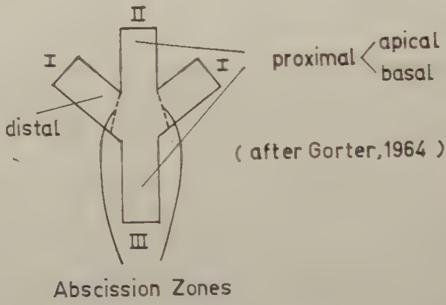
Jacobs (1962) emphasised, the translocation of the auxin in the tissue must be known in detail before we possibly can understand the results of investigations on the abscission of petioles of explants.

A previous study which revealed some characteristics of the transport of auxin in explants of *Coleus*, has been published elsewhere (Gorter and Veen, 1966). It was stated in that paper that almost all radioactivity remained in the tissue when the auxin (carboxyl-labelled naphthylacetic acid), was applied to the apical proximal end of the explants. More detailed information on the immobilization and the localization of auxin in the tissue of explants of *Coleus* will be given in the present paper.

MATERIAL AND METHOD

The material used has been described in detail by GORTER (1964). All material originated from a single clone of *Coleus rhenaltianus*, vegetatively propagated throughout the years. The plants were grown in the greenhouse.

The explants comprised a node with 5 mm pieces of stem above and below and two petiole stumps of 5 mm each (see Fig. 1). They were taken from the younger part of the plant where the apical proximal internode was about 10 mm long. These plants consisted of five internodes.



(after Gorter,1964)

Fig. 1. Scheme of an explant used in the experiments

The explants were placed horizontally in petri dishes on small foam plastic cushions. Each petri dish contained 5 explants. The dishes remained in the dark at 20° C.

The growth substance was applied in agar blocks (2 per cent) of 0.02 ml volume each placed on the apical or basal ends of the stem parts (position II and III resp.).

The α-naphthylacetic acid -1-^{14}C (NAA, carboxyl labelled) was obtained from The Radiochemical Centre, Amersham, England, and had a specific activity of 5.28 mc/mmole (28.4 μc/mg). Afterwards a new batch with a specific activity of 8.27 mc/mmole (44.5 μc/mg) was used. The compound appeared to be stable and showed no any radiochemical impurities as checked by thin layer chromatography with different solvent systems. The final concentration of the auxin in the agar donor blocks will be given together with the experiments.

Radioactive assay was done by the liquid scintillation counting technique. Agar blocks were transferred into small vials and equilibrated with 2 ml distilled water for 24 hours to permit diffusion of the radioactive substance from the blocks into the water. 1 ml of ethylalcohol was then added to the vials. The scintillation solution contained per litre:

800 ml dioxan
160 ml ethyleneglycolmonoethylether
48 g naphthalene
9.6 g 2.5-diphenyloxazole (PPO)
0.48 g 1.4-bis-2-(5-phenyloxazolyl)-benzene (POPOP)

The radioactivity in each vial was determined in a Packard Tri-Carb liquid scintillation spectrometer. Samples were counted for at least 10 minutes at 0° C. The counting efficiency in these experiments is 51 per cent for an aqueous standard of ^{14}C in the 100–1000 window at a high voltage setting of 1040 V. The background in our experiments was usually 45 cpm. All counting data were checked statistically on $P < 0.05$. Under these conditions 1 cpm corresponds to appr. 1.5×10^{-10} mmole NAA.

To measure the degree of quenching the counts are recorded in two separate channels. The ratio of these two channels provides a fast correlation with counting efficiencies determined with the aid of an internal standard. Quench correction is carried out by this channel ratio method, so that the addition of an internal standard to all vials is unnecessary.

The identity of the radioactive substances in the agar blocks as well as in the tissue was determined by thin layer chromatography. The blocks and tissue parts were frozen in dry ice and afterwards extracted for several hours with hot acetonitrile. The liquid was evaporated to dryness and the residue was taken up in 0.5 ml of acetonitrile. Extraction with acetonitrile was preferred to alcohol because it had been found by BACH (1961) that it gave almost quantitative extraction of radioactivity while it minimizes the extraction of other cell constituents. Moreover, acetonitrile is a free-radical quenching solvent, it is miscible with water, evaporates easily and is relatively non-toxic to plants (STOWE, 1963). The different samples were spotted on chromatograms of silica gel G and developed with isopropanol/ammonia 25 per cent/water (8:1:1). The chromatograms were covered with a "Melinex" polyester film (thickness 6.25 μ) to avoid chemical reactions on the film plate. A Kodak medical X-ray no screen film was then placed against the chromatogram ("sandwich"); the film was exposed for at least one week. After developing the films, places on the chromatogram that had given blackening on the film were marked and the silica gel from each area was carefully scraped off the glass and transferred to a Tri-Carb counting vial. The scrapings were suspended in 2 ml of distilled water and 1 ml of ethanol for several hours and regularly shaken to elute the organic material into the water. To this suspension was added the scintillation liquid. The radioactivity found at different spots on the chromatogram are expressed as a percentage of the total radioactivity extracted.

The total amount of the acetonitrile-soluble ^{14}C in the tissue pieces was measured by taking a sample of 0.1 ml of the final 0.5 ml extract. This sample was counted in the usual way.

The radioactivity, remaining in the tissue pieces after acetonitrile extraction was determined by grinding the tissue in a mortar in 2 ml of distilled water and 1 ml of ethanol. The final suspension was counted in the spectrometer in the usual way. The radioactivity extracted at the end of 5 hours by the water-ethanol mixture was 10–20 per cent of the amount of radioactivity extracted with acetonitrile. The chemical nature of this rest-radioactivity was not further investigated.

The use of a relatively polar solvent scintillation system such as dioxane-water prevents the adsorption of radioactive polar material on silica particles and thus losses by self-absorption (SNYDER, 1964). Like Snyder we found no counting loss caused by any substantial self-absorption in an aqueous sample of ^{14}C in the presence of silica particles, as is illustrated by the next data. A 10 μl sample of an aqueous standard (0.0528 μc/10 μl) was spotted on a thin layer of silica gel. Without chromatographing, the spot was scraped off and counted in the spectrometer. In this case we were able to recover 95.4 per cent of the radioactivity of the original sample. We then measured the recovery of chromatographed spots of the same sample. The ratio between the sum of all radioactivity present in the scrapings of a chromatogram and an aqueous sample directly pipetted into a counting vial provides us a check of the utility of the whole thin layer chromatography technique. The mean value of the recovery from four chromatograms was 91.3 per cent. From these data we concluded that thin layer chromatography in combination with liquid scintillation counting is an useful tool in the separation and quantitative determination of compounds labelled with ^{14}C.

The localization of the auxin at cellular level was studied by microautoradiography. Minute pieces of *Coleus* tissue were frozen in isopentane cooled with liquid nitrogen (— 175° C). The pieces were dehydrated at — 80° C with anh. acetone for 8 days. The acetone solution was refreshed every day. The acetone was replaced by a monomer metacrylate mixture to which was added a polymerisation initiator. This mixture was kept at a temperature of 2° C. Finally the small tissue pieces were placed in gelatine capsules filled with a metacrylate mixture. Heating at 60° C then starts the polymerisation. (For details see GIELINK, SAUER and RINGOET, 1966).

Sections 5 to 10 μ thick were cut on a rotating microtome. The slices were collected on glass slides, and a piece of stripping film (Kodak AR 10) was placed on the slides. An exposure time of 54 days usually gave the best results in this particular case. After this period the films were developed. Slices were studied by means of a Zeiss photomicroscope.

RESULTS

Some general data on auxin transport in *Coleus* explants have already been published (GORTER and VEEN, 1966). The results will be shortly summarized here:

By applying donor blocks (with auxin) and receiver blocks (plain agar blocks) in various positions, it was possible to make a simultaneous study of basipetal and acropetal transport in these explants. NAA translocation in *Coleus* tissue is mainly basipolar, but there is also some acropetal movement. The radioactivity found in the receivers at the basal proximal end (position III) after 10 hours of application of auxin at the apical proximal end (position III) is about 20 times that found in the receivers placed on the distal cut surfaces (position I).

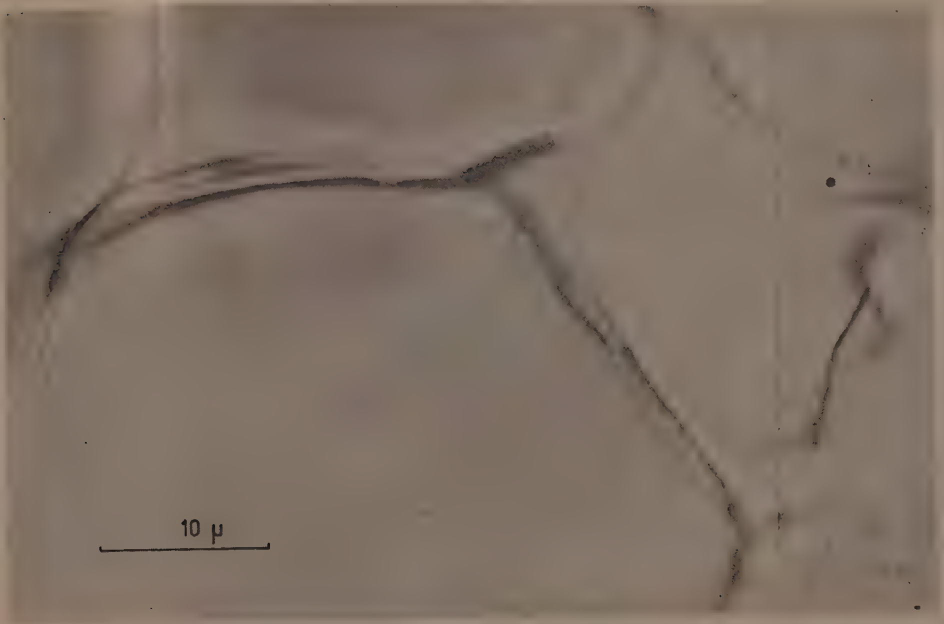


Fig. 2. Photograph focussed on the tissue.

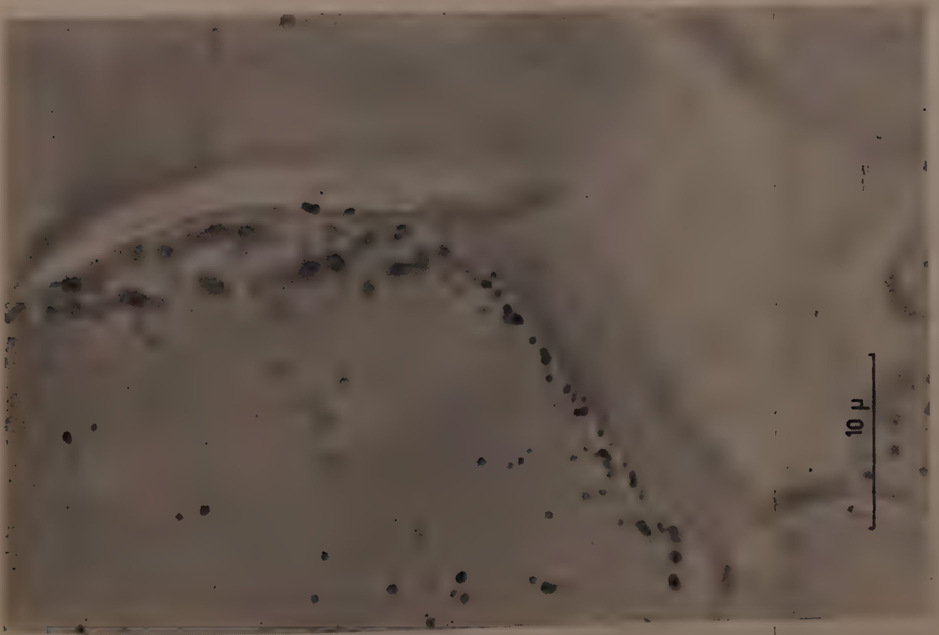


Fig. 3. Photograph focussed on the stripping film covering the slices

Figs. 2 and 3. Photographs of microautoradiograms showing radio-activity inside parenchymatic pith tissue of *Coleus* stem sections.

PLATE I

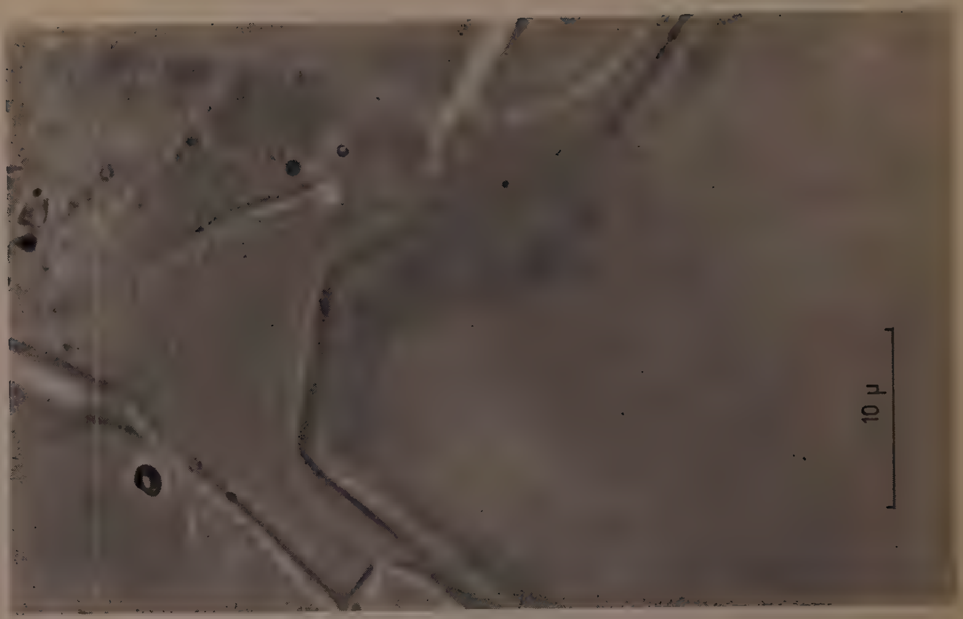


Fig. 4. Photograph focussed on the tissue.

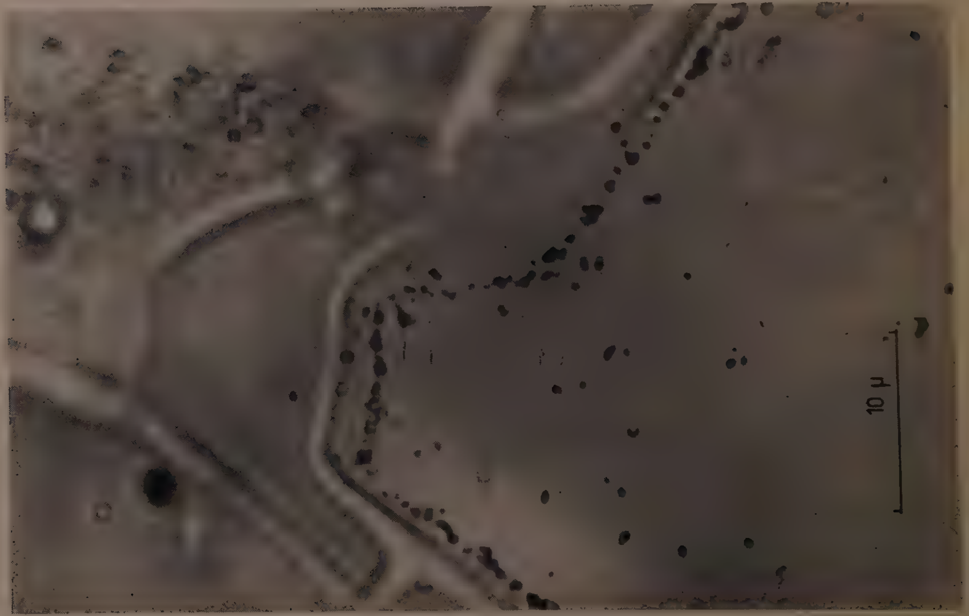


Fig. 5. Photograph focussed on the stripping film covering the slices.

Figs. 4 and 5. Photographs of microautoradiograms showing radio-activity inside parenchymatic pith tissue of *Coleus* stem sections.

PLATE II

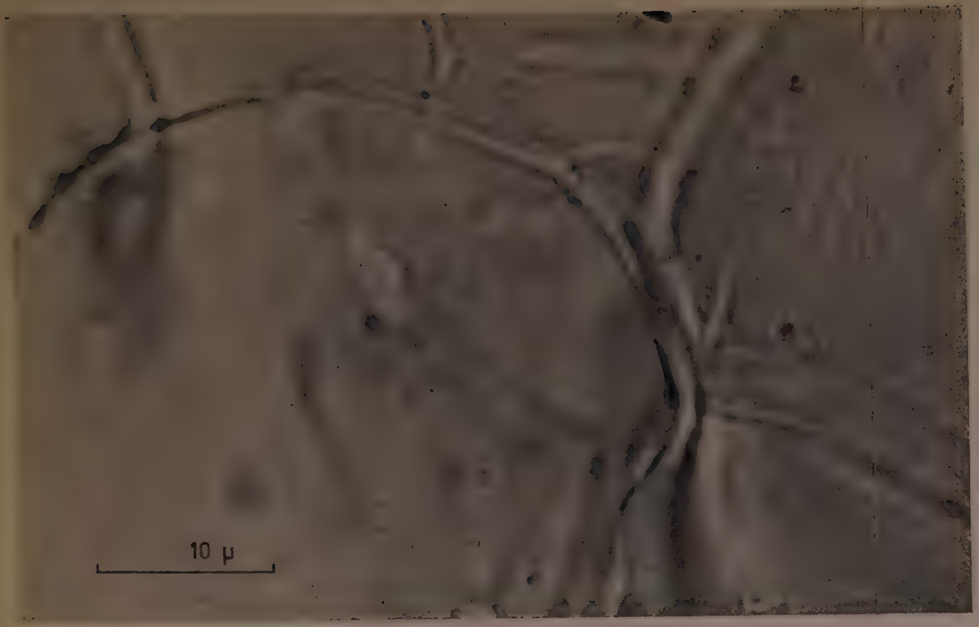


Fig. 6. Photograph focussed on the tissue; it shows plasmolysis.

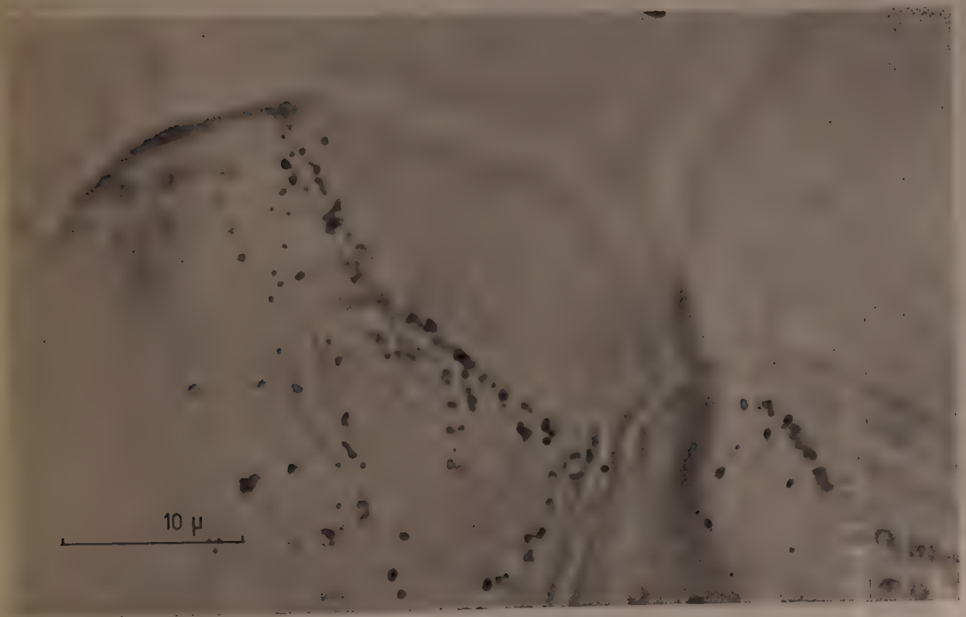


Fig. 7. Photograph focussed on the stripping film covering the slices; it shows plasmolysis.

Figs. 6 and 7. Photographs of microautoradiograms showing radio-activity inside parenchymatic pith tissue of *Coleus* stem sections.

PLATE III

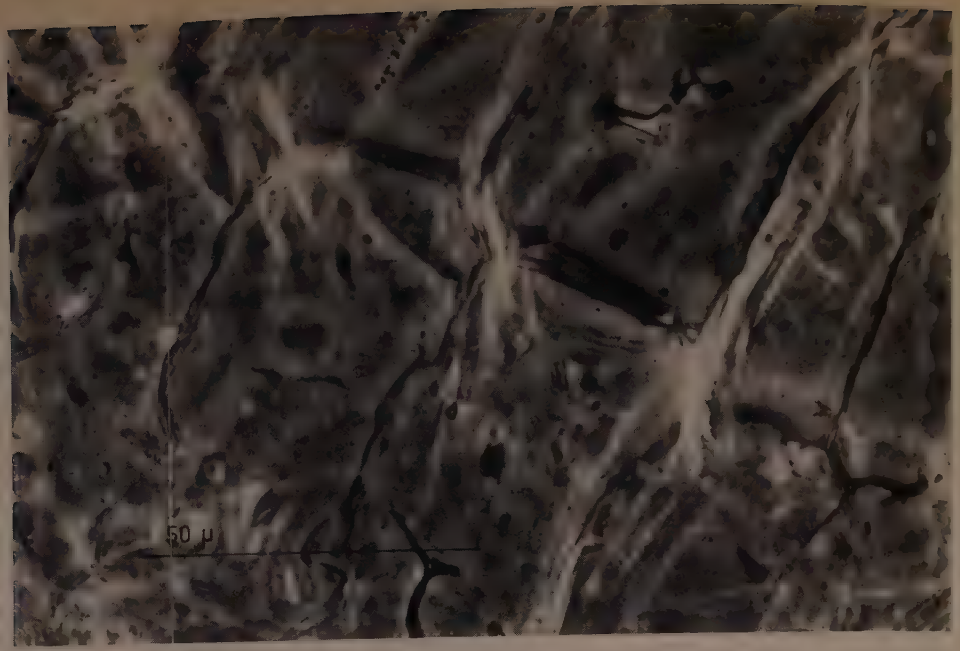


Fig. 8. Photograph focussed on the tissue, and made with phase contrast microscopy; it shows plasmolysis.

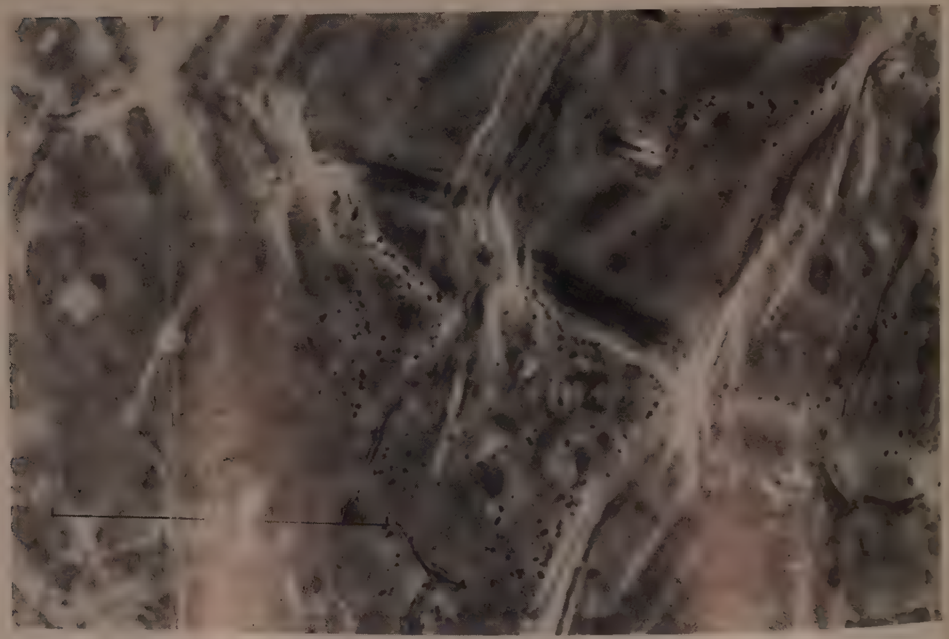


Fig. 9. Photograph, focussed on the stripping film covering the slices, and made with phase contrast microscopy; it shows plasmolysis.

PLATE IV

Increase of radioactivity in basal receivers is linear with time during the first 10 hours; after 10 hours a maximum is reached, after which the transport comes to a standstill. The activity in the basal receivers after 24 hours is only a very small percentage of that lost from donor blocks (viz. 1.4 per cent). Nearly all radioactivity is immobilized in the tissue.

From preliminary experiments we obtained good evidence that the decarboxylation rate of NAA by *Coleus* tissue can be neglected. This was studied by a manometric method described by YARDLEY (1964). In the first 6 hours the amount of free $^{14}CO_2$ in the atmosphere is less than 0.1 per cent of the initial concentration. We therefore concluded that nearly all radioactivity which entered the tissue is fixed in the explant. To study the gross distribution of the radioactivity in the explant we carried out the following experiment. Donor blocks (conc. 2.4×10^{-4} M) were applied to the apical proximal end of the explant. After 24, 48, 72 and 96 hours the explants were divided into different parts:

part 1 = apical proximal part
part 2 = petiole stumps
part 3 = the node
part 4 = basal proximal part.

These parts were extracted and the radioactivity counted as described earlier. The data are given in Table 1.

From the data of Table 1 we conclude that about three quarters of the total gross radioactivity fixed in the explant is retained in the 5 mm apical proximal part below the donor block.

The intracellular localization of the radioactivity in this part of the explant was further studied by microautoradiography. Hitherto reports have been published of two methods of localising growth substances at the cellular level. The first was applied by THIMANN and BETH (1959). They removed the potential site of action from cells to which auxin was applied afterwards. This was done with *Acetabularia* from which the nucleus had been removed. A clear effect

TABLE 1

Gross distribution of acetonitrile-soluble ^{14}C after auxin application at the apical proximal part of the explant. Donor Conc. $= 2.4 \times 10^{-4}$ M. Extractions after 24, 48, 72 and 96 hours. Explants were divided in Part 1: apical proximal part, part 2: petiole stumps, part 3: the node, part 4: basal proximal part. Results are given as cpm per mg dry weight and as percentages of the total extracted radioactivity of a whole explant.

Part	Time in hours							
	24		48		72		96	
	cpm	%	cpm	%	cpm	%	cpm	%
1	9881	69.7	17135	72.8	21207	81.0	16061	75.8
2	382	1.8	111	0.3	71	0.2	97	0.3
3	744	12.0	1002	9.0	1026	8.3	1338	11.6
4	1130	16.4	2197	17.8	1370	10.5	1639	12.3

of auxin was found even on the enucleated cells. The second method was applied by Galston and Kaur (1959). Auxins labelled with radioactive isotopes were applied to cells which were fractionated by centrifugal forces in an attempt to determine into which part of the cell the auxin had found its way. The conclusion to be drawn from such studies is that auxin does not bind itself to any of the cell particles and that its site of action may be in the nonparticulate phase of the cytoplasm (Galston and Purves, 1960).

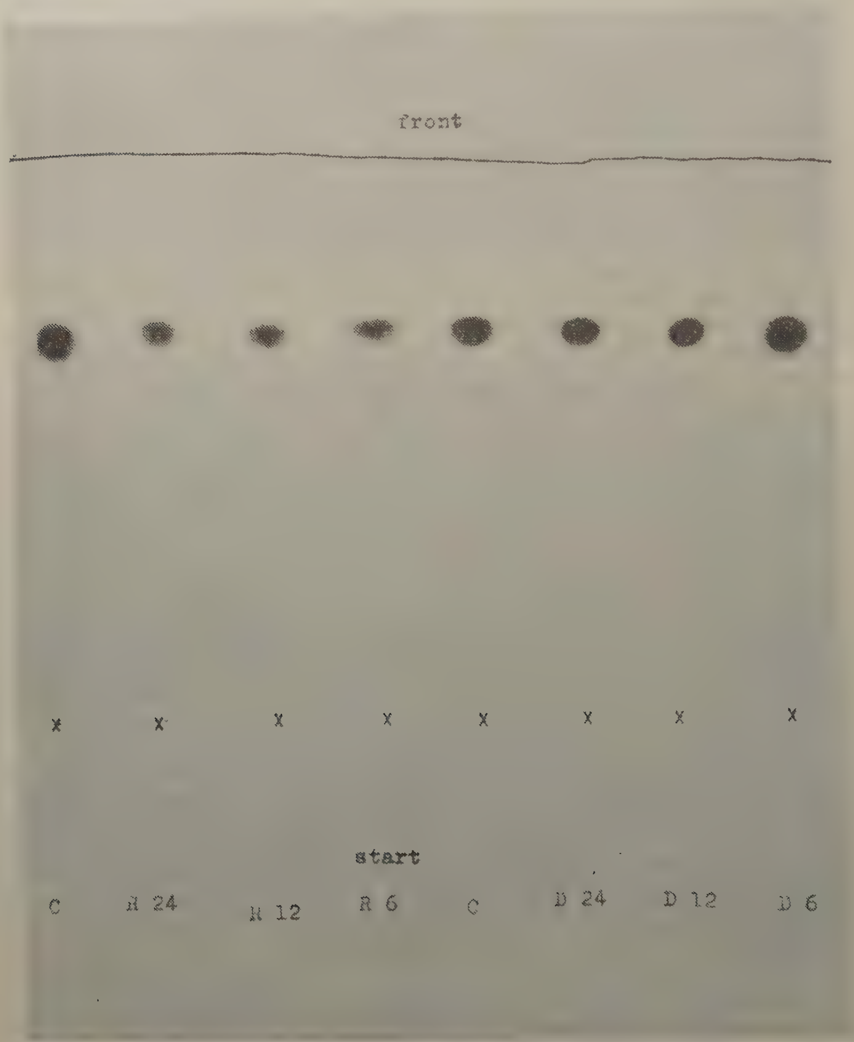


Fig. 10. Photograph of a Kodak no screen X-ray film, which had covered a thin layer chromatogram for about a week. After 6, 12 or 24 hours only one compound can be recovered in receiver and donor blocks with a *Rf*-value, which is the same as NAA-^{14}C (c).

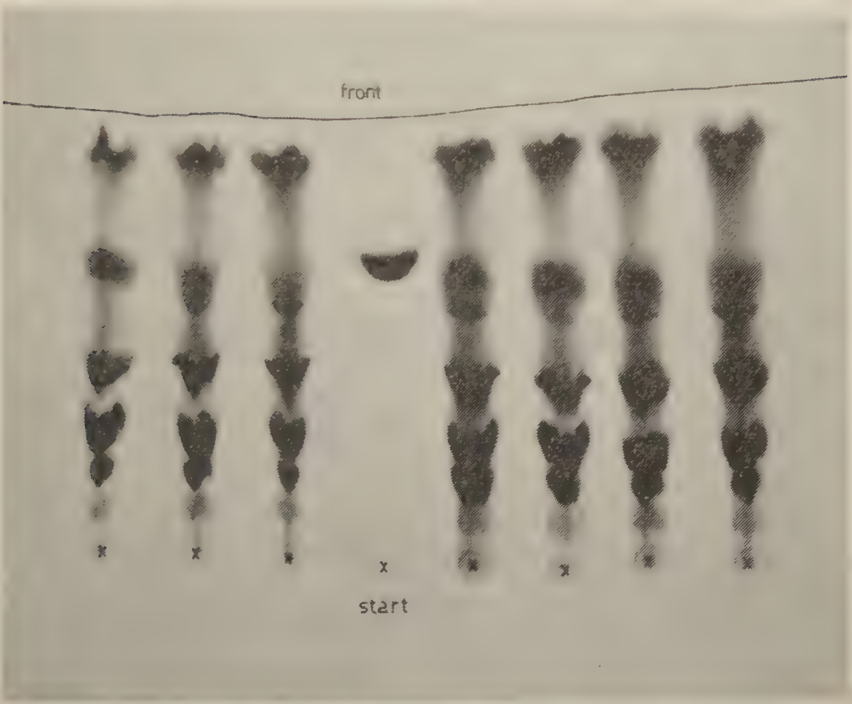


Fig. 11. Photograph of a Kodak no screen X-ray film, which had covered a thin layer chromatogram for about a week. NAA is converted into at least six other compounds. All the spots were of identical extracts made after 24 hours.

There is also clear evidence from many other experiments that auxins are attached to some receptor entity in the cell, although it is possible that the labelled auxin is so weakly attached that the link is soon broken by centrifugation. For this reason it seems necessary to locate the site of action by other methods, e.g. microautoradiography. Therefore the next experiment was carried out. NAA-^{14}C was applied to the cut end of the apical proximal part of explants of *Coleus*. The donor concentration was about 4×10^{-4} M NAA. After 24 hours the apical proximal part of the explant (in which the bulk of the radioactivity is fixed) is divided in small parts of appr. 1 mm and treated further for autoradiography as described earlier.

These microautoradiograms clearly demonstrate the presence of radioactivity in the cytoplasm next to the cell wall, as is shown in the Figs. 2–9. As a rule two photographs were taken of each object, the first focussed on the tissue, the second on the film. In one case some plasmolysis could be observed; here the blackening of the film exactly followed the cytoplasm. It should be remembered that these photographs were taken from longitudinal slices of the central pith of the apical proximal part of a *Coleus* explant. Cross-sections of the same tissue produced a more intense blackening per unit of area above the cortical tissue than above the pith tissue. But in the cortical part

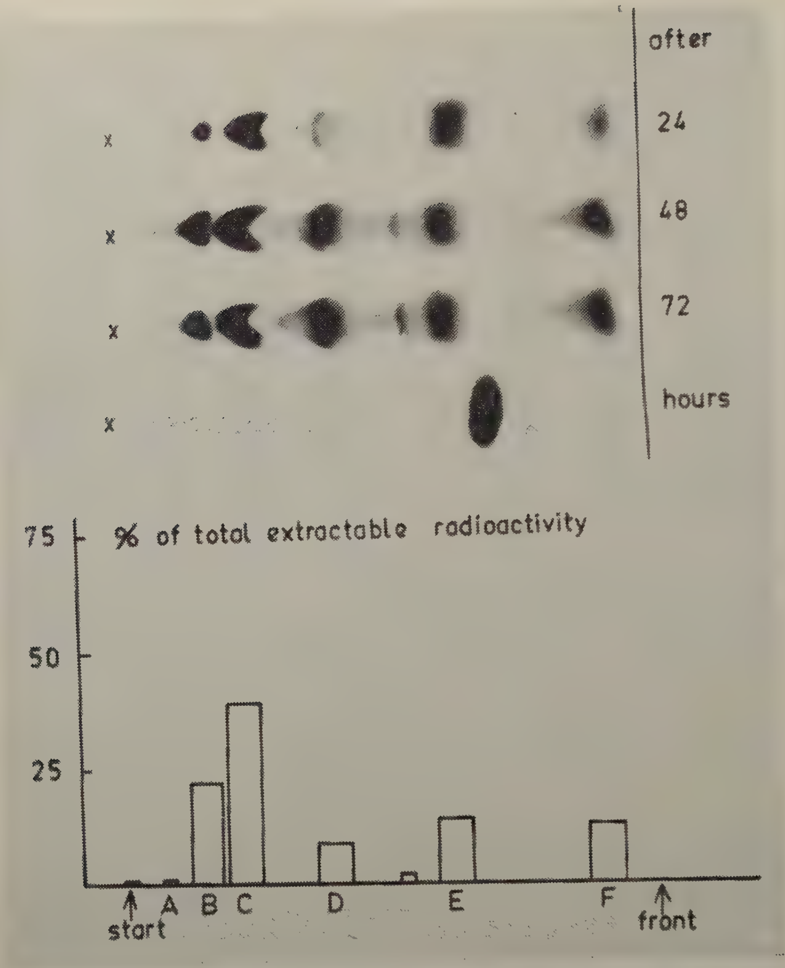


Fig. 12. The radioactivity at different spots on the chromatograms, expressed as a percentage of the total extracted ^{14}C material. The upper part of the figure shows a film which covered the thin layer chromatogram for about a week, the lower part gives the radioactivity found at each spot expressed as a percentage of the total amount of radioactivity extracted by acetonitrile. Only the data of the 24-hour experiment are plotted.

of the sections, the intracellular localization of the radioactivity was not so distinct.

Jacobs (1965) recently showed that for IAA and 2, 4, — D the transport velocity was the same in both pith tissue and "cortical tissue" (which included the vascular tissue). For both auxins more net loss was observed into cortical tissue than into pith tissue. Jacobs explains this by the difference in cell number; the cortical tissue contains ten times as many cells as the pith tissue, although the areas are identical. The difference between the blackening of the parts of the film which were above the cortical and the pith tissue, as found in our own experiments, can be explained in the same way.

According to previous published evidence (GORTER and VEEN, 1966), only NAA could be detected in receiver blocks after 6, 12 and 24 hours (see Fig. 10). But chromatography of an extract of a whole explant some hours after application of the auxin already showed a conversion into several compounds (see Fig. 11).

The radioactivity found at different spots on the chromatogram is expressed as the percentage of the total acetonitrile-soluble ^{14}C-material. This is shown in Fig. 12, the upper part of the figure being an example of an autoradiograph from chromatograms obtained by placing a film on the thin layer chromatogram and the lower part showing the radioactivity found at each spot of the chromatogram expressed as the percentage of the total amount of radioactivity extracted by acetonitrile. In this particular case only the data of the 24 hours experiment are plotted.

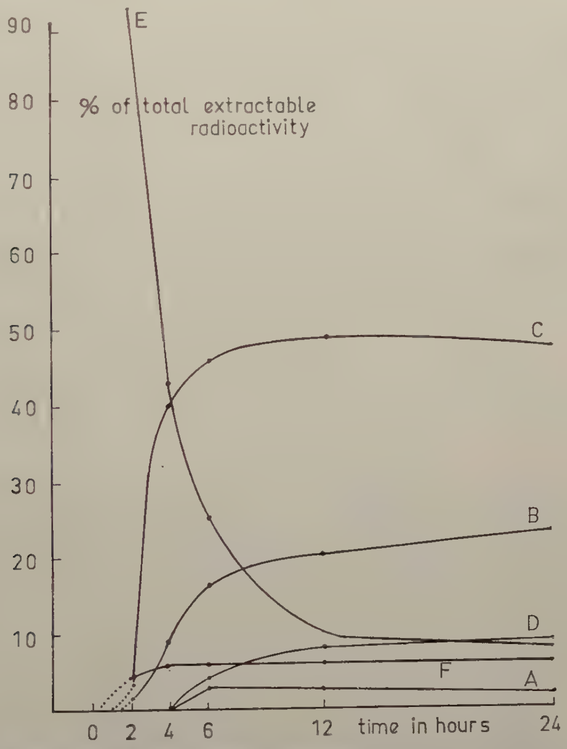


Fig. 13. The amounts of the various compounds in tissue extracts, expressed as a percentage of the total extracted radioactivity, in relation to the time.

The relative amounts of the various compounds (cf. Fig. 11) were determined at different times after application of the auxin at the apical end of the explants. Donor conc. was 4 × 10^{-4} M. After 2, 4, 6, 12 and 24 hours the donor blocks were removed and the whole explant was extracted. The extracts were chromatographically analysed in the usual way the results being shown by Fig. 13. A striking feature is the rapid decrease of the extractable amount of compound E. After 6 hours only 25 per cent of the original amount

TABLE 2

Gross distribution of acetonitrile-soluble ^{14}C and the relative amounts of some metabolites in two different regions of an explant. Apical proximal part means the apical stem end of the explant just below the donor block. Donor Conc. 2 × 10^{-4} M. The basal proximal part means the basal stem end of the explant at a distance of 25 mm from the donor block. Extractions were made after 24, 48, 72 and 96 hours. The gross distribution is given as cpm per mg dry weight. The amounts of the different compounds are given as the percentages of the total extracted radioactivity present in apical and basal parts resp.

	Gross distr.	Comp. E probably NAA	Comp. C probably NAAsp	Comp. F probably NAAglu
Apical prox. part				
time	cpm	%	%	%
24	12043	10.7	53.2	11.5
48	17554	5.8	48.3	10.2
72	18376	6.0	39.4	13.5
96	16869	3.8	39.2	8.4
Basal prox. part				
time	cpm	%	%	%
24	220	48.0	15.1	19.0
48	113	30.9	3.8	32.2
72	130	26.9	13.0	28.3
96	105	31.2	14.8	24.0

TABLE 3

A comparison of the R_{NAA}-values, which represent the movement of the unknown compounds relative to NAA, present on the same chromatogram. The *Rf*-values of the different compounds found in our experiments is also given in the table together with the postulated chemical identity of the compounds.

Compound	*Rf*-value	R_{NAA}-value			postulated chem. identity *)
		Klämbt	Zenk	Veen	
A	0.07	—	—	0.11	—
B	0.15	0.23	0.25	0.23	8–OH–1–NAAglu.
C	0.22	0.18	0.28	0.34	NAAsp
C′	0.30	—	0.52	0.47	—
D	0.36	0.65	0.57	0.56	8–OH–NAA
D′	0.40	—	—	0.62	—
D″	0.55	0.75	—	0.86	—
E	0.64	1	1	1	NAA
F	0.87	1.30	1.22	1.36	NAA-glu.
F′	0.93	—	1.22	1.45	—

*) For abbreviations see text.

of compound E is left. The Rf-values of compound E and pure NAA are the same. This strongly suggests that both substances are identical. Another remarkable feature is the rapid increase in the amount of extractable compound C, and to a lesser degree of compound B. Only relatively small amounts are formed of the compounds A, D and F. The decrease in compound E (i.e. NAA) in the tissue and the simultaneous increase in a number of unidentified compounds suggests that NAA is converted to other substances in the tissue.

We next studied the conversion of NAA at different parts of the explants. GORTER (1964) found that the abscission of the petioles of explants was influenced by the length of the proximal parts (above or below the node). This might be explained by assuming a difference between auxin transport and/or metabolism in explants with long or short proximal parts. In view of the results obtained by Gorter we studied the translocation and the metabolism of NAA in explants of which the proximal basal part was 25 mm instead of the usual 5 mm. Donor blocks (2×10^{-4} M) were applied to the apical proximal part. After 24 hours the apical proximal parts (5 mm) and the most basal proximal parts of 10 mm were collected and extracted as described before. After 24 hours the apical proximal parts contained a gross radioactivity of 12000 cpm per mg dry weight, whereas the basal proximal parts only contained 220 cpm per mg dry weight. Chromatographic analysis of the two extracts showed a substantial difference between the ratios of the various compounds in both extracts. Table 2 shows that in the basal part NAA is present as such for nearly 50 per cent (10 per cent in apical part), while compound F is present in a relatively greater amount than compound C, this situation being the reverse of that in the apical proximal part. This difference in metabolic turnover continues for a period of 96 hours (see Table 2). It may be ascribed to the different absolute amounts of radioactivity in the two parts, or it may be an ageing effect (unpublished results); the basal part of the stem is older than the apical part of the stem of the same explant.

Only one of the compounds present in the acetonitrile-soluble fraction has so far been identified. Compound C was hydrolyzed with HCL and chromatographed again. The radioactivity was then recovered at a much higher Rf-value than before treatment and was equal to that of NAA itself, while we could demonstrate a ninhydrin positive spot on the same chromatogram, close to the Rf-value of aspartic acid. Hence compound C is very probably identical with naphthylacetyl aspartic acid. By comparing the data of ZENK (1962) and KLÄMBT (1961) with our own data it is possible to postulate the chemical nature of the other compounds. We therefore calculated the R_{NAA}-values, i.e. the movement of a compound relative to NAA, present on the same chromatogram. These are shown in Table 3. Since the compounds A, B, C, D, E and F together represent more than 90 per cent of the total extracted radioactivity, we will only consider these 6 compounds.

Compound A has not previously been identified.

Compound B might be identical with the glucose ester of 8-hydroxy naphthylacetic acid (8 OH-1-NAAglu). This compound was isolated and identified by Klämbt (1961b). The phenolic OH-group is bound as a β-glucoside, so that the molecule has a free acid group like NAA itself.

Compound C is identified as naphthylacetyl aspartic acid (NAAsp). Klämbt (1961a) and Zenk (1962) proved the presence of this compound in various plant tissues.

Compound D might be identical with 8-OH-naphthylacetic acid (8-OH-NAA). Like Klämbt, Zenk (1962) assumes that a part of the radioactive NAA is converted into hydroxylated NAA, which may be partly bound to glucose.

Compound E is naphthylacetic acid (NAA).

Compound F, finally, might be identical with naphthyl acetyl β-d-glucose (NAA-glu). This glucose ester was identified by Klämbt (1961a) as well as by Zenk (1962).

Some of these compounds are detoxication products, others may be related to growth phenomena. In the discussion attention will be paid to the biological consequences of the observed metabolic turnover of NAA in Coleus explants.

Discussion

No attempt will be made to discuss all the literature relating to auxin transport in plant tissue. The reader is referred to Leopold (1963). It has already been demonstrated (Gorter and Veen, 1966) that all radioactivity in receiver blocks is from naphthylacetic acid. Therefore it seems logical to assume that the radioactivity in the transport system is not subject to metabolic conversions. One should distinguish between auxin in the transport system and auxin fixed in the cytoplasm and thus withdrawn from the amount of auxin transported. The immobile auxin, so-called auxin pool, consists among other materials, of complexes of auxin with sugars and aspartic acid. It has not yet been established whether or not free NAA still present in tissue in which these complexes are formed is transportable.

Auxin transport in *Coleus* sections is saturated at a donor concentration of 2 to 5 mg per litre (Scott and Jacobs, 1963). Their experiments lasted only 2½ hours. After such a short period at least 80 per cent of the acetonitrile-soluble ^{14}C fraction is still present as NAA (see Fig. 13). It therefore seems unlikely that this saturation phenomenon can be explained by the removal of auxin from the transport system by immobilization, as was suggested by Goldsmith and Thimann (1962). Our own theory is that all sites in the "secretion unit" are occupied at a concentration of over 2 to 5 mg per litre. Arguments supporting the concept of such a 'secretion unit' are adduced by Hertel and Leopold (1963). If this unit is occupied, the auxin concentration in the tissue next to the receiver block will increase and pass a hypothetical threshold value required for enzyme induction. Experiments to prove the presence of a threshold value are now in progress.

The adaptive enzyme system which is formed will conjugate aspartic acid to an auxin molecule by establishing a peptide link between the carboxyl group of the auxin and the amino group of the aspartic acid molecule. The formation of this compound shows a lag period of more than 2 hours (see Fig. 13). The adaptive formation of NAAsp (Zenk, 1962; Südi, 1964) means a "de novo" synthesis of an unnatural enzym system. The inducer (NAA) acts catalytically in the formation of the enzyme and not stoichiometrically (Dixon and Webb, 1960). We may therefore expect a certain donor concentration of the auxin above which induction occurs. Auxin is immobilized in the plant tissue by this enzyme system. This immobilization may explain why after 10 hours no more auxin is secreted out of the tissue into the receiver blocks. The concentration of free auxin in the transport system in the tissue next to the receiver block, decreases to such a low value that no further transport of auxin can be observed.

Goldsmith and Thimann (1962) found that the concentration of radioactivity in a section of an *Avena* coleoptile declines exponentially with the distance from the source. In agreement with these observations we noticed a retention of radioactivity in the first 5 mm below the source up to 70 per cent of the total acetonitrile-soluble ^{14}C in the explant present after 24 hours. The microautoradiographic photographs show that this radioactivity is fixed in the cytoplasm next to the wall. Efforts to localize auxin shortly after application, in an attempt to pinpoint the transport pathway, have so far been unsuccessful so that our results give no definite answer about the route by which auxin is transported in the tissue.

The metabolism of indoleacetic acid was first studied by Andreae and co-workers (1955, 1956, 1957 and 1961) in pea root tips. They isolated indoleacetyl aspartic acid and indoleacetamide. The latter product appeared to be an artefact according to Klämbt (1961a) and Zenk (1961 and 1962). Besides indoleacetyl aspartic acid, indoleacetyl-β-d-glucose was found in plant extracts (Klämbt, 1961a; Zenk, 1961). Klämbt also isolated several hydroxy-auxins viz. 2-hydroxy indoleacetic acid and 8-hydroxy naphthylacetic acid (Klämbt, 1959 and 1961b). The β-d-glucosides of these hydroxy-auxins are present to a much larger extent than the free hydroxy-auxins (Klämbt, 1964). The author suggests that the hydroxylation may be a prerequisite for the auxin activity in the cell.

As the pattern of the metabolites of indoleacetic acid and naphthylacetic acid is very similar it may be safe to compare these two auxins (Klämbt, 1961a).

By comparing R_{NAA}-values we postulated the identity of some of the NAA metabolites formed. We are well aware of the doubts expressed about the real value of this method, but as we used the same solvent system as Zenk and Klämbt a comparison of *Rf*-values is useful.

In agreement with Zenk (1964) the amount of NAAgl (substance F) increases without a lag period, see Fig. 13, in contrast with that of naphthylacetyl aspartic acid, which shows an adaptation period of 2 hours. As we could completely reproduce the findings of Zenk (1964), we may quote his conclusion here: "the formation of the glucose ester of the auxin seems to be a mechanism for very rapid detoxification of aromatic carbonic acids during a time when the conjugation-system utilising aspartic acid is being adapted in the plant. The glucose ester is not stable in the cell after the aspartic acid-conjugating system has been adapted, but becomes eventually transformed into the auxin-aspartic acid complex. Finally there is a certain amount of free auxin in the cell, which is not exchangeable with auxin in the medium and which is protected from further metabolic alterations." Zenk's last conclusion is supported by the data of Table 2. Even after 4 days still 4 per cent of the total extracted radioactivity is still present as NAA. This percentage is even higher in tissue parts with a very small amount of gross radioactivity. In such a tissue the amount of the auxin-glucose ester is higher than the aspartic acid conjugation, which remains over a period of 4 days, as can be seen in Table 2. We fully agree with Zenk's conclusion that the formation of the glucose ester precedes the auxin-aspartate formation; however, if the gross amount of extracted "auxin" remains very small the glucose ester will be present in larger amounts for a longer period.

Zenk does not assume that the NAA-aspartate conjugation and the glucose-ester formation plays an essential part in the growth induction mechanism. He stated that both conjugates are true detoxication products.

According to KLÄMBT (1964) hydroxy-auxins may be connected with growth phenomena. He stated that the occurrence of hydroxylated auxins in the plant substantiates Muir and Hansch's theory on the mode of action of growth hormones (MUIR and HANSCH, 1953). This concept will not be discussed further.

If compound B is identical with the glucose ester of 8-hydroxy naphthylacetic acid and compound D with the hydroxy-auxin itself, we agree with Klämbt that the glucosides of these auxins are present to a much larger extent than the free hydroxy-auxins themselves (see Figs. 12 and 13).

Although we have no arguments to support the concept of Siegel and Galston on the formation of a complex between auxin and a macromolecule (SIEGEL and GALSTON, 1953), it cannot be rejected. 10 to 15 per cent of the initially applied amount of auxin remains in the tissue after extraction with acetonitrile and with an alcohol-water mixture, and is unidentified. A detailed study of this fraction would seem to be called for.

No attempt will be made at present to relate the results described in this paper to such phenomena as geotropic – and epinastic curvatures, rooting and abscission of petioles, although this will be the goal of further investigations.

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THE ALKALI CATION CARRIER OF BARLEY ROOTS: A MACROMOLECULAR STRUCTURE?

G. G. J. BANGE AND C. L. C. MEIJER

(*Mineral Nutrition Research Group, Botanical Institute of the University of Leyden, The Netherlands*)

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ABSTRACT

Excised barley roots were allowed to absorb Rb and Cs from single or mixed Rb- and Cs-chloride solutions of various concentrations in the presence of 10 me/l $CaSO_4$. Absorption periods of 3 and 6 hours respectively enabled the separate estimation of the steady rate of uptake setting in after about 3 hours and the additional amount of cation absorbed within the first 3 hours, which is supposed to represent cation bound to protoplasmatic binding sites. The following results were obtained.

1. The absorption and competition behaviour of Rb and Cs at different concentrations cannot be understood on the basis of the view that the binding sites involved in the absorption of these ions are separate and completely independent units.
2. In some important features there is a close though not absolute similarity between the effect of concentration on the steady rate of absorption of Rb and Cs after 3 hours, on the one hand, and on the additional amount of Rb and Cs absorbed within the first 3 hours, on the other.

The bearing of these results on our notions concerning the nature of the carrier mechanism is discussed, and a structural conception of the association between ion and carrier advocated.

1. INTRODUCTION

The kinetic approach applied in ion uptake studies has appeared useful in elucidating mechanisms underlying competition behaviour (e.g. BANGE, 1959; BANGE, TROMP and HENKES, 1965) or distribution patterns (e.g. BANGE and VAN VLIET, 1961), but it may seem questionable whether this type of work can contribute to the identification of "carrier" substances supposedly involved in the transport process. It seems to us that such doubt is unjustified. In this paper we will present kinetic data that, in our view, may contain an important clue to the nature of the cell constituents involved in alkali cation transport in barley roots.

The leading thought behind this work was that if ion carriers are relatively simple chemical compounds entering into a reversible binding reaction with the ions to be transported, then the competition between such ions as Rb and Cs must proceed strictly according to kinetic formulae analogous to those developed for enzyme reactions when two substrates compete for the same active site on an enzyme molecule (cf. EPSTEIN and HAGEN, 1952). It will be shown below that the kinetic behaviour of Rb and Cs uptake is much more complex than can be explained on the basis of any such relatively simple reaction scheme.

Another observation could be brought to bear upon the tentative conclusions drawn from this fact. With respect to some striking features, an unmistakable similarity was found in the dependence on external concentration of steady-state Rb and/or Cs absorption on the one hand and the amount of these ions present in a kinetically defined cell compartment as described by HOOYMANS (1964) and tentatively identified by her with the cytoplasm, on the other.

It will be brought out that in our view the evidence obtained suggests that in the binding and transport of the alkali cations a macromolecular structure rather than some relatively simple chemical compound is involved.

2. MATERIAL AND METHODS

2.1. *Plant material*

Excised roots of barley (*Hordeum vulgare* L. cultivar. "Herta") were used throughout these experiments.

Fifty grams of seed were disinfected for two minutes with a 1 % $HgCl_2$ solution and rinsed in flowing tapwater for three hours. They were then soaked for about 20 hours in aerated tapwater at 25° C, washed with demineralized water, and spread evenly on a stainless-steel screen covered by a piece of aseptic gauze and supported by a perspex frame. The frame was placed in a plastic tray containing about 4 litres of 2×10^{-4} M $CaSO_4$ solution, which was aerated continuously; the gauze dipped into the solution at all sides of the frame. The tray was placed in an airconditioned dark room (temperature 25° C, relative humidity about 70 %) for 7 days. During this period the $CaSO_4$ solution was renewed three times at regular intervals.

2.2. *Experimental procedure and analytical methods*

Before the start of an experiment the roots were cut at a point between the gauze and the steel screen and rinsed in three changes of 4 litres of aerated demineralized water for 10 minutes each. After washing, the roots were wrapped in gauze and centrifuged for three minutes at low speed to remove the adhering water.

Equal portions of root material, varying from 0.5 to 3.0 grams according to experimental conditions, were weighed out and transferred to polyethylene bottles containing 10 litres of experimental solution. Air was bubbled through the solutions and their temperature maintained at 25° C by a waterbath. At the end of the experimental period the roots were collected by pouring the solutions over a filter of nylon mesh, washed for 1 minute with flowing demineralized water, and transferred to crucibles.

After drying at 85° C, the roots were ashed at 560° C and the ash dissolved in diluted HCl. After digestion for a quarter of an hour on a hot plate, the solutions were filtered and the filtrate made up to 50 or 100 ml.

The concentrations of Rb, K, and Cs were estimated with a Beckman

Model DU flamephotometer at wave lengths of 780, 766, and 852 mμ respectively.

2.3. *Experimental solutions*

The alkali cations were supplied throughout as their chlorides. Apparently, the RbCl (CsCl) used was not completely free of contaminating Cs (Rb) since in some experiments in which only RbCl (CsCl) was present, a small increase in the Cs (Rb) content of the roots was demonstrated. To all experimental solutions, $CaSO_4$ (B. D. H. "AnalaR") was added in a concentration of 5×10^{-3} M. No special precautions were taken to control the pH of the solutions because it was not deemed desirable to add buffering substances. Under such circumstances the actual pH value may vary between 5.2 and 5.6.

3. RESULTS

3.1. *Uptake of Rb and Cs in relation to time*

It has been demonstrated by HOOYMANS (1964) that the establishment of a steady state in alkali cation uptake in excised root material is complicated by two circumstances. In the first place, in the absence of Ca at pH values of about 5.5 the rate of K uptake shows a gradual decline with time which can be abolished by the addition of an appropriate amount of Ca to the experimental solutions. In the second place, except at very low concentrations after about 2½ hours the initial rate of K and especially Rb uptake in the presence of Ca changes rather abruptly into a new and lower value that is maintained for the rest of the experimental period.

To eliminate the first complication, we performed all experiments in the presence of 5×10^{-3} M Ca. The effectiveness of this procedure is demonstrated by Fig. 1 A, which shows that for Rb as well as for Cs after 2½ hours a constant rate of uptake sets in. This holds for separate Rb and Cs solutions (Fig. 1 A) as well as for mixtures (Fig. 1 B).

As to the second complication, which appears to be very pronounced in the case of Rb as well as of Cs, it was ascertained that in compliance with the conclusions of HOOYMANS (l.c.) the decline in the rate of uptake after about 2½ hours is not due to the onset of an efflux: when after 4 hours Rb is replaced by an equal concentration of K (Fig. 1 C) the Rb content of the roots remains at the level attained. The rate of uptake (in me/hr) setting in after about 2½ hours, and which for convenience we will refer to as steady-state uptake, was determined by subtracting total uptake over 3 hours from total uptake over 6 hours and dividing the number of milliequivalents obtained by three. The same data allow the estimation of the amount of additional cation uptake during the initial period of 2 or 2½ hours, by the subtraction of steady-state uptake from total uptake in the first period of 3 hours. For instance, when in 3 hours 16 and in 6 hours 25 me Rb/kg fresh weight of roots have been absorbed, the rate of steady-state uptake is $(25 - 16)/3 = 3$ me Rb/kg-hr and the

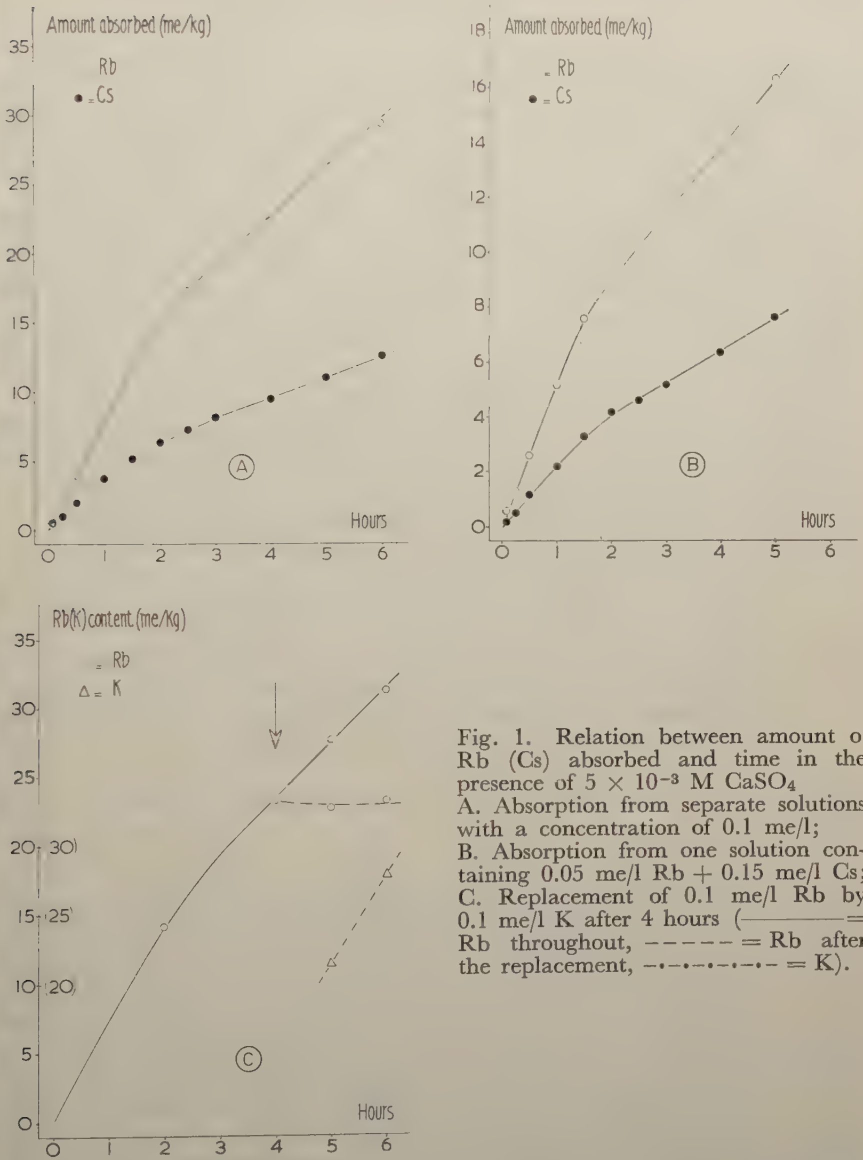


Fig. 1. Relation between amount o Rb (Cs) absorbed and time in the presence of 5×10^{-3} M $CaSO_4$
A. Absorption from separate solutions with a concentration of 0.1 me/l;
B. Absorption from one solution containing 0.05 me/l Rb + 0.15 me/l Cs;
C. Replacement of 0.1 me/l Rb by 0.1 me/l K after 4 hours (——— = Rb throughout, – – – – – = Rb after the replacement, –•–•–•–•– = K).

excess Rb absorbed during the initial period ("fraction I" in the terminology of Hooymans) 16 — (25 — 16) = 7 me Rb/kg.

It should be noted that the excess amount of Rb and Cs absorbed during the first 2½ hours has nothing to do with Rb or Cs present in the so-called A(pparent) F(ree) S(pace) of the tissue. Actually in the time curves shown neither a W(ater) F(ree) S(pace) nor a D(onnan) F(ree) S(pace) manifests itself by an intercept on the ordinate what may be ascribed to the relatively long final rinsing of the roots with demineralized water and the presence of excess divalent cation in the experimental solutions.

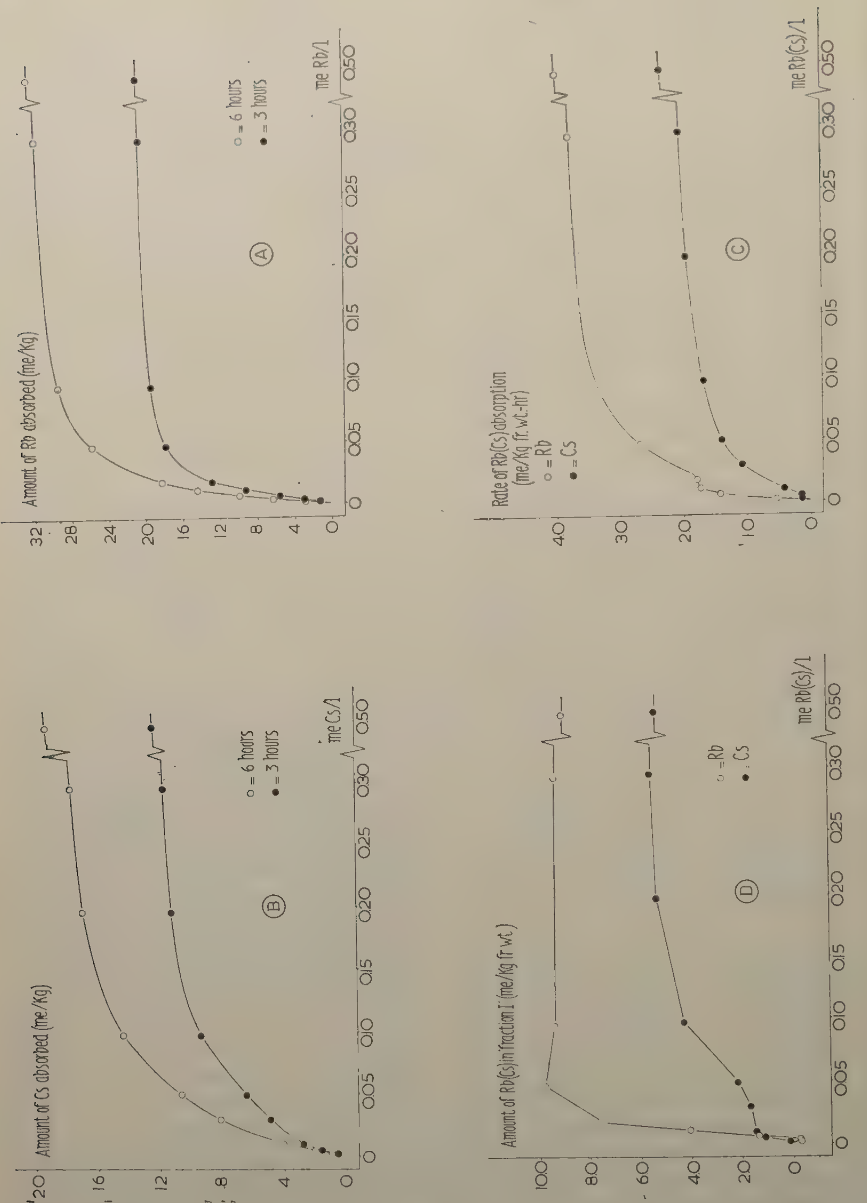


Fig. 2. The effect of concentration on the rate of steady-state Rb and Cs absorption and on the amount of Rb and Cs present in fraction I
A. Amount of Rb absorbed within 3 and 6 hours in the range of concentrations from 0 to 0.5 me/l. Data represent the average of 3 separate experiments;
B. The same for Cs;
C. Calculated rates of steady-state Rb and Cs absorption;
D. Calculated amounts of Rb and Cs present in fraction I.

3.2. *Uptake of Rb and Cs in relation to concentration*

The amount of Rb and Cs absorbed in 3 and 6 hours in the range of concentrations from 0 to 0.5 me/l is shown in Figs. 2 A and 2 B respectively. Calculated rates of steady-state absorption are given in Fig. 2 C, and calculated Rb and Cs contents of fraction I in Fig. 2 D.

The important features of these graphs are the following.

1. The relation between steady-state Rb uptake and Rb concentration (Fig. 2 C) cannot be described by some simple mathematical equation. The curve breaks up into a steep initial part and a portion rising more slowly to the level of saturation. Between these parts a point of inflection seems to occur in the curve, a feature that is manifest in all of the three experiments from which the data presented in Fig. 2 C have been averaged.
2. The same holds for the inflection point indicated at the lowest Cs concentrations (Fig. 2 C). Quite apart from this complication, the remarkable feature of the absorption curve for Cs is that the absorption level at saturation is nearly twice as low as for Rb.
3. With increasing concentration the amount of Rb as well as Cs in fraction I attains a saturation level (Fig. 2 D) that again for Cs is almost twice as low as for Rb. For Rb this saturation is reached at a much lower concentration than for Cs. No Rb is accumulated in fraction I at the lowest concentrations, which corroborates the observation of Hooymans (l.c.) that at low Rb concentrations Ca has the effect of straightening out the uptake versus time curves. A considerable part of the final amount of Cs present in fraction I seems to be accumulated at very low Cs concentrations.

3.3. *Competition between Rb and Cs: varying Rb concentration, constant Cs concentration*

In a first series of competition experiments (Fig. 3, A, B, and C) the concentration of the inhibiting ion (in this case Cs) was maintained at 0.1 me/l, whereas the concentration of the inhibited ion (Rb) was varied from 0 to 0.4 me/l. Total uptake within 3 and 6 hours is shown in Fig. 3 A, the rate of steady-state absorption in Fig. 3 B, and the amount accumulated in fraction I in Fig. 3 C.

A direct comparison between Figs. 3 B and 2 C is hampered by the fact that for different batches of roots absolute rates of uptake may vary. Therefore, all rates of Rb as well as Cs absorption have been expressed as percentages of the rate of Rb uptake at a Rb concentration of 0.1 me/l in the presence of 0.1 me/l Cs (Fig. 5 A). Because of the larger variability in the results concerning the amount of Rb and Cs in fraction I, no attempt has been made to apply the same procedure to these data.

The salient features of the competition behaviour in the steady-state phase of absorption (Figs. 3 B and 5 A) are the following.

1. There is a marked but gradually declining inhibition of Cs absorption per unit increment of Rb concentration.
2. Rb uptake is not hampered by the presence of Cs at low

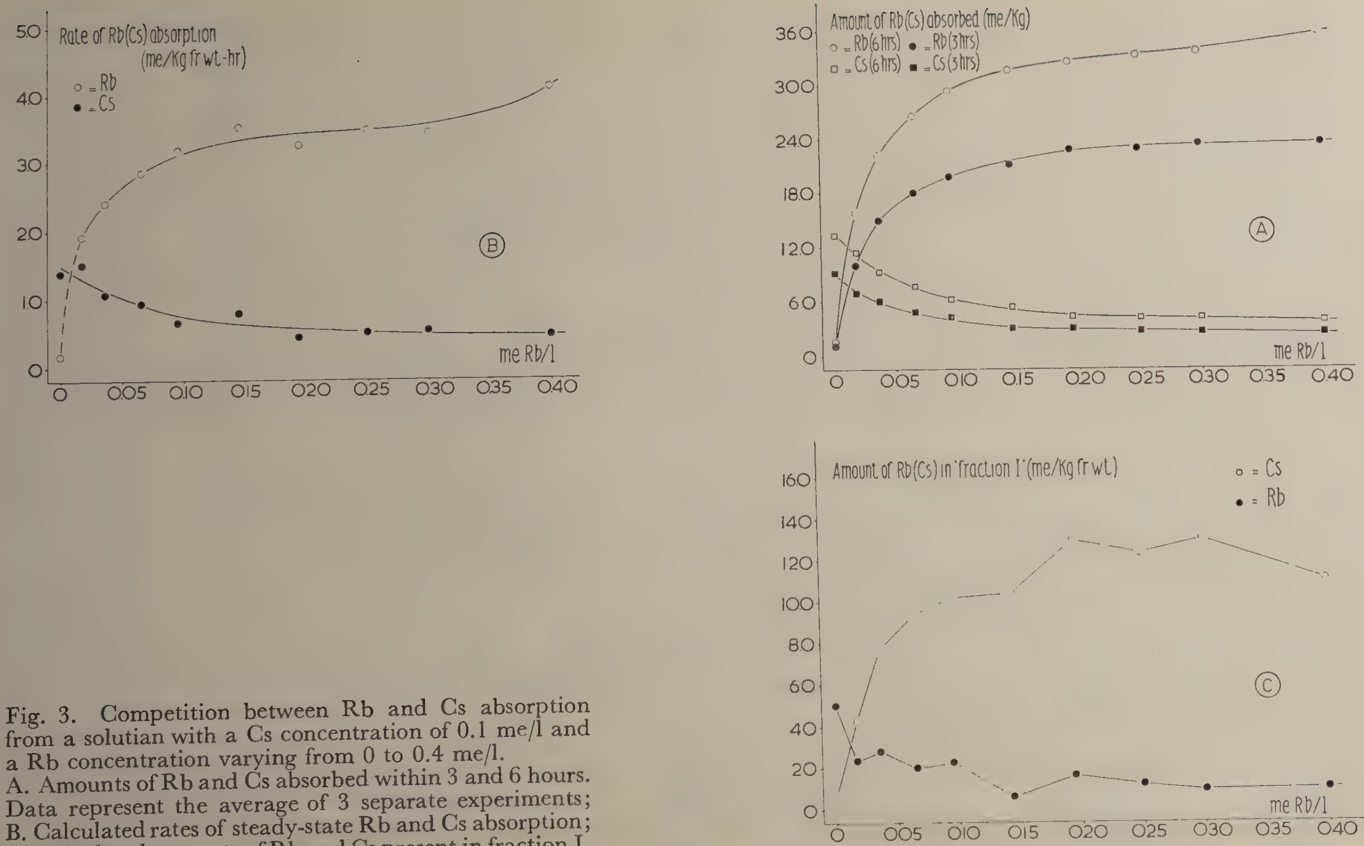
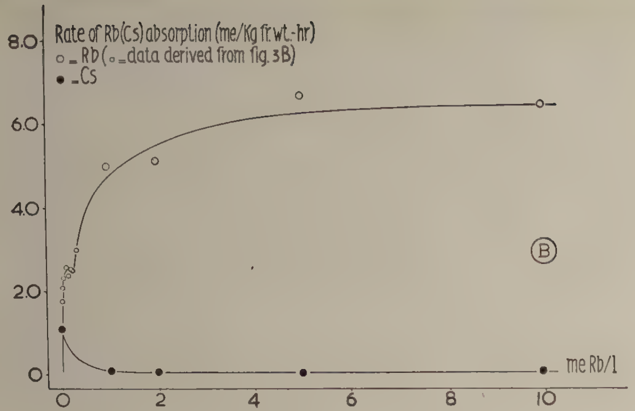


Fig. 3. Competition between Rb and Cs absorption from a solutian with a Cs concentration of 0.1 me/l and a Rb concentration varying from 0 to 0.4 me/l.
A. Amounts of Rb and Cs absorbed within 3 and 6 hours. Data represent the average of 3 separate experiments;
B. Calculated rates of steady-state Rb and Cs absorption;
C. Calculated amounts of Rb and Cs present in fraction I.



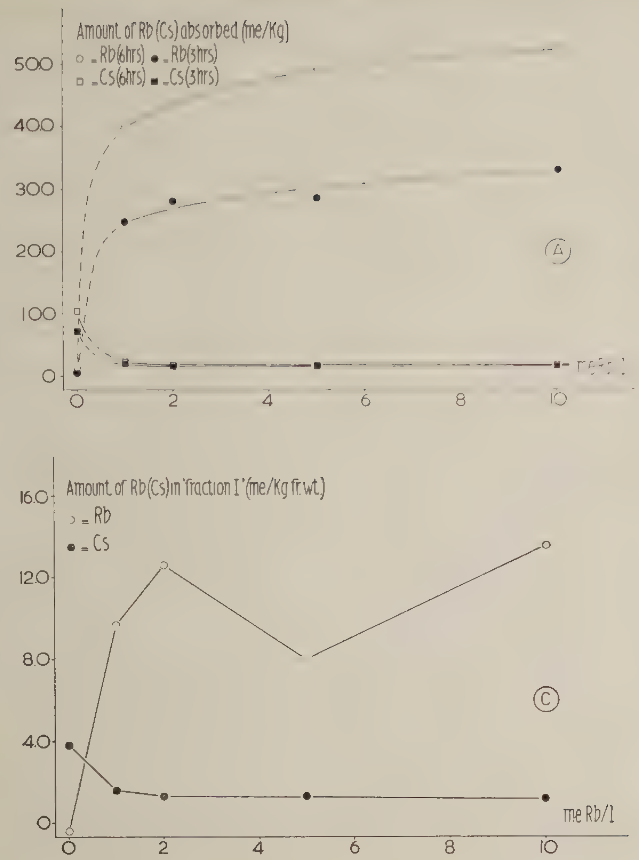


Fig. 4. Competition between Rb and Cs absorption from a solution with a Cs concentration of 0.1 me/l and a Rb concentration varying from 0 to 10 me/l
A. Amounts of Rb and Cs absorbed within 3 and 6 hours. Data are from a single experiment;
B. Calculated rates of steady-state Rb and Cs absorption. Small circles represent data from Fig. 3B reduced to the absolute scale of Fig. 4B by means of the ratio of absolute rates of uptake of Cs at 0.1 me/l in the absence of Rb;
C. Calculated amounts of Rb and Cs present in fraction I.

concentrations (0.015 me/l). As to the part of the curve above the inflection point, it is not so much the general shape as the relative saturation level attained in this concentration range that appears to be affected by the presence of Cs.

3. There is a close similarity between the competition behaviour of steady-state Rb and Cs absorption and the uptake of Rb and Cs into fraction I (Fig. 3, B and C).

In a second, not duplicated, experiment the Rb concentration was raised up to 10 me/l at the same constant Cs concentration of 0.1 me/l (Fig. 4, A, B, and C). In accordance with the disproportionate increment in Rb absorption at 0.4 me/l Rb in Fig. 3 B, another inflection

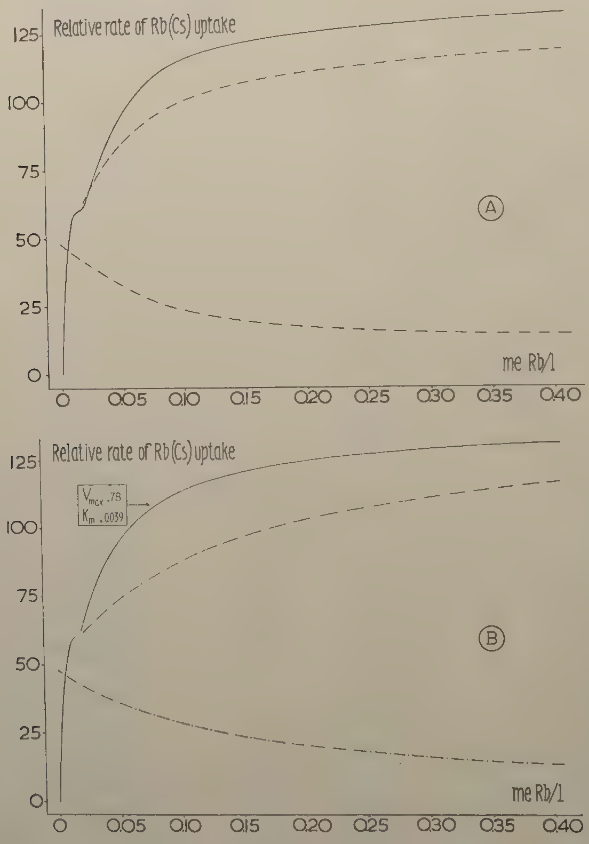


Fig. 5. A. Rate of Rb absorption at various concentrations in the absence (——) and presence (– – – –) of 0.1 me/l Cs, and concomitant Cs absorption (–•–•–•–) on a comparable scale (see text);
B. Theoretical competition curves for the case of a two-site uptake mechanism for Rb, one of which is common to Cs and Rb. Denotations as in Fig. 5A. For further explanation, see text.

point appears to lead to a new and still higher saturation level of steady-state Rb absorption (Fig. 4 B). At the same time, Cs uptake sinks to the very low level of about 0.05 me/kg fresh weight per hour, which is maintained even at the highest Rb concentrations. The same feature is still more conspicuous in the amount of Cs present in fraction I (Fig. 4 C), thus demonstrating once more the impracticability of checking all Cs absorption by the supply of an excess of a competing ion. No marked increase in the Rb content of fraction I at high Rb concentrations is indicated (cf. Figs. 4 C and 3 C).

3.4. *Competition between Cs and Rb: varying Cs concentration, constant Rb concentration*

In the next series of competition experiments the concentration of Rb as the inhibiting ion was kept constant at 0.1 me/l, whereas Cs concentration was varied from 0 to 0.4 me/l (Fig. 6: data averaged from three separate experiments) and from 0 to 10 me/l (Fig. 7: data from a single experiment). Total uptake within 3 and 6 hours is shown in Figs. 6 A and 7 A, the rate of steady-state absorption in Figs. 6 B and 7 B, and the amount accumulated in fraction I in Figs. 6 C and 7 C. Finally, in complete analogy to Fig. 5 A, Fig. 8 A contains the data from Fig. 2 C and Fig. 6 B recalculated relative to the same standard uptake as used for Fig. 5 A.

The following features of the competition behaviour in the range of low concentrations (Figs. 6 B and 8 A) are noteworthy.

1. In the presence of a constant Rb concentration Cs uptake rises more slowly with concentration and to a lower relative saturation level than in the absence of Rb.

2. From a Cs concentration of 0.2 me/l to 0.4 me/l there is a marked reduction in the rate of Rb absorption without a concomitant rise in the rate of Cs absorption.

3. Competition for uptake into fraction I appears to proceed along lines similar though not identical to the characteristics of competition in the steady-state phase of absorption (Fig. 6, B and C).

When the Cs concentration is raised to 10 me/l, the rate of Cs absorption rises above the relative saturation level attained in Fig. 6 B, and reaches a new maximum (Fig. 7 B). Here too, an inflection point seems indicated at a concentration of about 0.5 me/l. At the same time, after an initial steep fall, Rb absorption keeps declining slowly in the range of concentrations from 2 to 10 me/l though unaccompanied by an equivalent rise in Cs uptake.

Again the same general features are apparent in the amount of Cs and Rb in fraction I (Fig. 7 C). However, even at the highest Cs concentrations the amount of Rb in fraction I is not reduced anywhere near so strongly as steady-state Rb absorption. The same phenomenon was encountered in Cs inhibition by excess Rb (see under § 3.3).

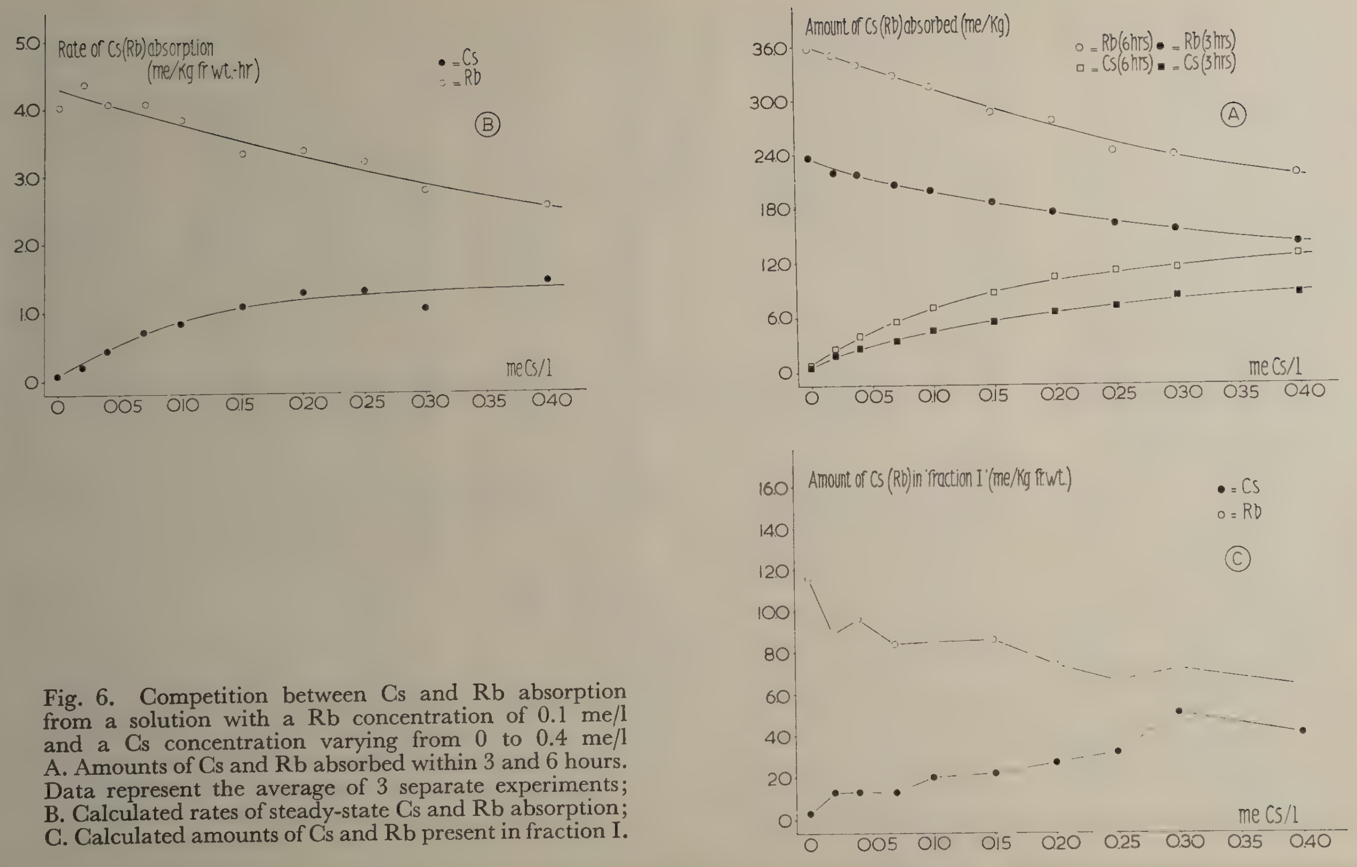


Fig. 6. Competition between Cs and Rb absorption from a solution with a Rb concentration of 0.1 me/l and a Cs concentration varying from 0 to 0.4 me/l A. Amounts of Cs and Rb absorbed within 3 and 6 hours. Data represent the average of 3 separate experiments; B. Calculated rates of steady-state Cs and Rb absorption; C. Calculated amounts of Cs and Rb present in fraction I.

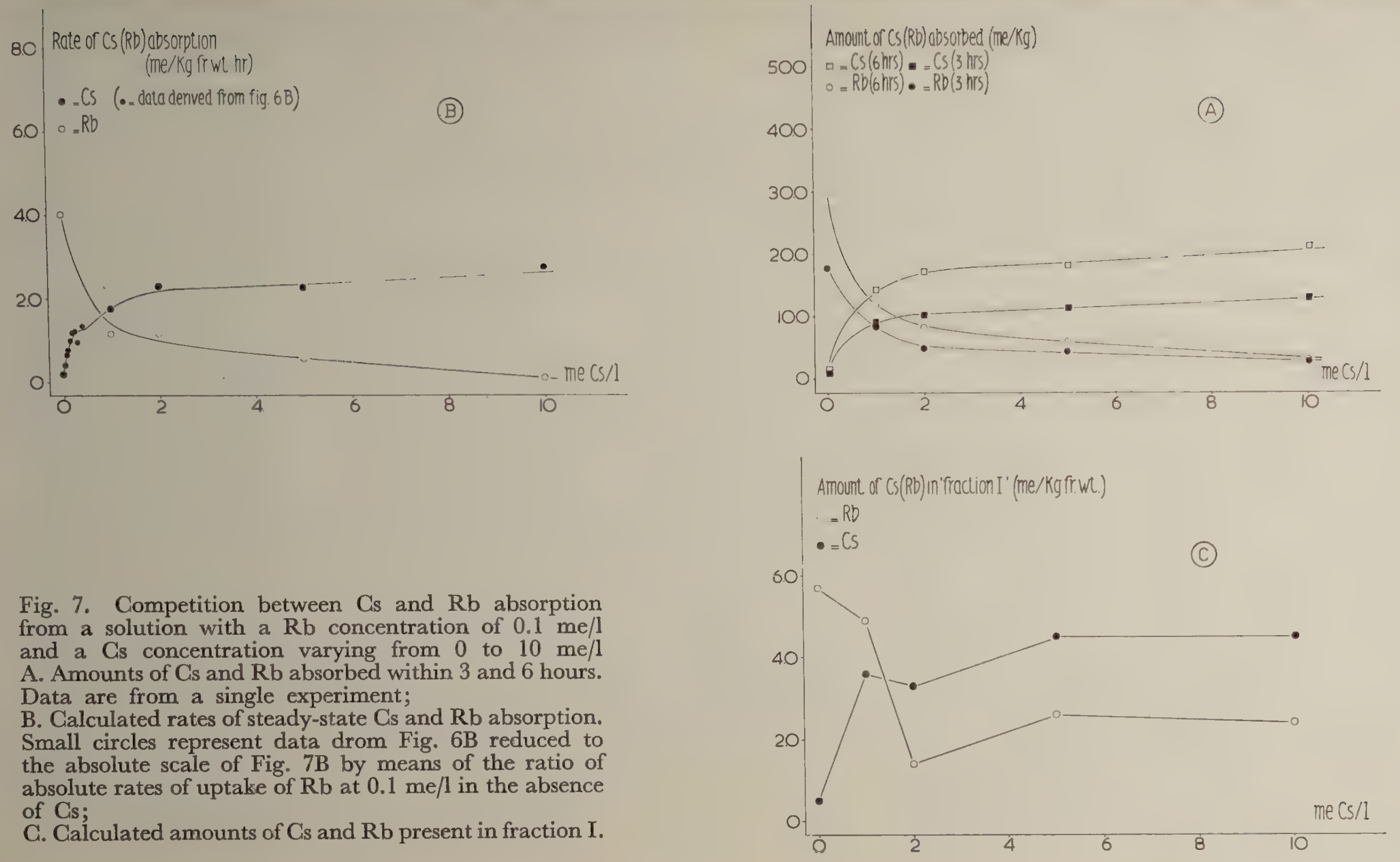


Fig. 7. Competition between Cs and Rb absorption from a solution with a Rb concentration of 0.1 me/l and a Cs concentration varying from 0 to 10 me/l
A. Amounts of Cs and Rb absorbed within 3 and 6 hours. Data are from a single experiment;
B. Calculated rates of steady-state Cs and Rb absorption. Small circles represent data drom Fig. 6B reduced to the absolute scale of Fig. 7B by means of the ratio of absolute rates of uptake of Rb at 0.1 me/l in the absence of Cs;
C. Calculated amounts of Cs and Rb present in fraction I.

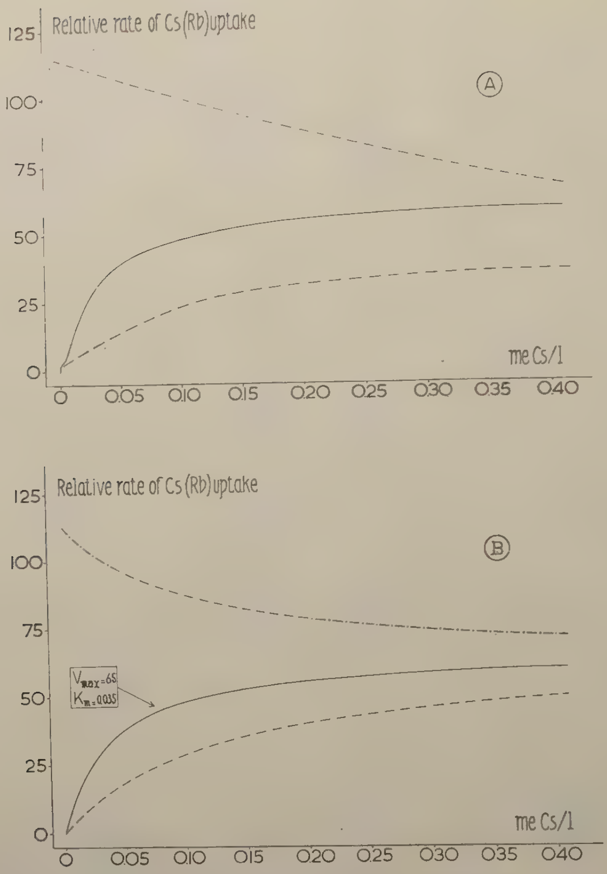


Fig. 8. A. Rate of Cs absorption at various concentrations in the absence (——–) and presence (– – – –) of 0.1 me/l Rb, and concomitant Rb absorption (–•–•–•–) on a comparable scale (see text); B. Theoretical competition curves for the case of a two-site uptake mechanism for Rb, one of which is common to Cs and Rb. Denotations as in Fig. 8A. For further explanation, see text.

4. Discussion

4.1. *Kinetic considerations*

As mentioned in the Introduction, the main purpose of this work was to ascertain whether or not the absorption behaviour of Rb and Cs fits into a kinetic pattern corresponding to the initial binding of these ions to identical sites of a carrier mechanism. For plant roots the principles of carrier kinetics have been worked out by Epstein and Hagen (1952) to which paper may be referred for further details.

We at once meet the difficulty that no simple kinetic scheme is able to explain the occurrence of inflection points in the absorption curves for Rb and – to a less extent – Cs (Fig. 2 C). Even when two or more independent binding sites are involved in the absorption of an ion, the slope of the relation between the over-all rate of uptake and concentration should decline continuously. It should be mentioned that similar inflection points have also been reported by other workers (EPSTEIN, 1964; ELZAM, 1964).

In the second place, we have to account for the fact that the rate of Cs uptake is only about one half of the rate of Rb uptake (Fig. 2 C). Two explanations present themselves.

1. Cs is transported by the same binding site as Rb but the rate of breakdown of the complex between the Cs-ion and the carrier is only about one-half of the corresponding value for Rb.
2. There are two binding sites, both of which transport Rb but only one of which transports Cs.

The first explanation is based on the assumption that only one common binding site is involved in Rb and Cs transport. It was demonstrated (Fig. 5 A) that at low Rb concentrations (up to about 0.02 me/l) Rb uptake is not inhibited by the presence of 0.1 me/l Cs. Taking into account the fact that Cs uptake is almost saturated at 0.1 me/l, in case of one common binding site this lack of inhibition should imply a sharp concomitant drop in Cs absorption. The actual decrease in Cs uptake is only about 15 %.

The alternative explanation seems more attractive because, as discussed under Material and Methods, § 2.2., the relation between Rb uptake and concentration consists of two distinct parts (Fig. 5 A). If it is assumed that the steep initial part reflects binding of Rb by a site with a high affinity to this ion but hardly any affinity to Cs, whereas the second part rising more slowly to relative saturation represents binding to a site with about equal affinities to Rb and Cs, not only the lower level of saturation of Cs absorption but also the lack of inhibition of Rb uptake at low Rb concentrations and the absence of a concomitant drop in Cs uptake in the competition experiment of Fig. 5 A might be explained. However, a close examination of the quantitative relations to be expected in case of the proposed mutual "competitive inhibition" reveals that such a mechanism cannot underly the experimental behaviour described (Figs. 5 B and 8 B).

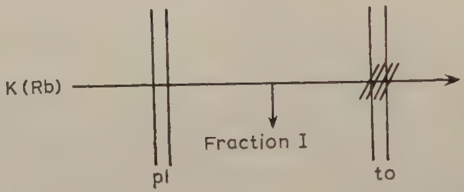
The curves in Figs. 5B and 8B have been constructed with the use of the formula for competitive inhibition given by EPSTEIN and HAGEN (l.c.). The K_m and K_i values required were derived from the absorption curves in the absence of an inhibiting ion. On account of the inflection in the uptake curve for Rb (Fig. 5A), the line ($x = 0.019$) had to be used as an ordinate in the mathematical description of the second part of this curve.

Quite apart even from such quantitative considerations, the considerable drop in Rb uptake in the competition experiment shown in Fig. 6 B (cf. Fig. 8 A) in the range of concentrations from 0.2 to 0.4 me/l Cs, unaccompanied by so much as half a proportional rise in Cs uptake, seems irreconcilable with any explanation based on a strictly competitive behaviour of the ions. The fact that absorption of Cs as well as Rb can be reduced to very low values by higher concentrations of the inhibiting ion (Figs. 4 B and 7 B) does not detract from this conclusion because the crucial question is whether or not purely competitive effects alone are able to explain our results.

The inference seems justified that the characteristics of Rb and Cs interaction do not fit the rigorous pattern of competitive inhibition kinetics.

4.2. *Steady-state absorption and uptake into fraction I*

HOOYMANS (l.c.) has presented evidence in favour of the view that the uptake of cations into fraction I represents binding of the ions to cytoplasmatic constituents. Although differing in some details, essentially the same view is held by FOOTE and HANSON (1964) who observed a similar biphasic time curve in K uptake by soybean roots after removal of two-thirds of the calcium of the tissue by treatment with EDTA. HOOYMANS (l.c.) assumes that in the presence of Ca the supply of K(Rb) to these cytoplasmatic sites is mediated by the steady-state absorption mechanism, the rate-limiting step of the latter occurring at the tonoplast and not at the plasmalemma, according to the diagram:



pl = plasmalemma to = tonoplast /// = rate-limiting step

In the experiments presented above we pointed out the remarkable though not absolute similarity with regard to concentration dependence and competition behaviour existing between the rates of steady-state absorption of Rb and Cs on the one hand and the amounts present in fraction I on the other. It might be argued that the quantity of Rb or Cs accumulated in fraction I in the presence of Ca is not representative of a true state of equilibrium between environmental alkali cation concentration and cytoplasmatic sites because of the inhibiting effect Ca has on the saturation of these sites at Rb concentrations below about 0.02 me/l (cf. 3.2.). However true this may be, it does not detract from such parallel features in Figs. 2 C and 2 D as the attainment of saturation in the concentration range from 0.1 to 0.5 me/l for Rb as well as for Cs, and, above all, the saturation level being about twice as high for Rb as for Cs. In the competition experiments the total concentration of Rb + Cs exceeded 0.1 me/l from the outset, so in this case these effects mav have been absent or at least of minor importance.

The parallelism observed seems of some consequence for our notions concerning the nature of the substance supposedly involved in alkali cation transport. From Fig. 2 D it appears that as much as 10 me Rb per kg fresh weight of roots may be present in fraction I. If this fraction is correctly identified with uptake into the cytoplasm or parts of it and the amount of cytoplasm is estimated at roughly 10 % of the fresh weight of the tissue, the cytoplasmatic Rb concentration proves to be 100 me/l. Therefore, the important conclusion to be drawn from this part of our observations seems to be that sites with binding characteristics closely akin to those of the cell components responsible for alkali cation transport, must be quite abundant in the cell.

4.3. *The possible nature of the substances involved in alkali cation transport*

Rather than raising doubts about the fundamental correctness of the concept of carrier-mediated cation transport, the discrepancies observed may serve the purpose of shaping its rather vague and simplified general formulation.

The anomalies revealed in the absorption and competition curves seem to make it inevitable that the idea of a system of binding sites working quite independently and without any mutual interference, is discarded. Although far from pretending to be able to give an alternative detailed explanation of the data presented, we hold the opinion that a better understanding of the facts observed becomes possible if two essential properties are attributed to the transport system, to be formulated as follows.

1. The separate sites binding the alkali cations are part of a larger unit (e.g. a protein molecule).
2. This unit does not have a structure so rigid as to remain unaffected by the presence or absence of ions at the binding sites as well as by the nature of the ions bound. In other words, binding fo an ion to one site may exert a strong influence on the structural properties determining the conditions under which similar or other ions are bound to adjacent sites.

It is noteworthy that in enzymology comparable "allosteric" effects have been claimed for the explanation of certain types of interaction between enzymes and their substrates or inhibitors (cf. Monod, Wyman, and Changeux, 1965). In fact, the un- and non-competitive types of inhibition introduced into the field of ion absorption by Epstein and Hagen (1952) may be looked upon as oversimplified examples of the type of structural interferences we have in mind.

Is it feasible, for instance, that the fundamental feature underlying the uptake behaviour of Cs as compared to Rb, consists of such a structural interference of adjacent sites as to prevent their simultaneous association with a Cs-ion, thus explaining the lower saturation level of Cs absorption? And could the same allosteric effect be responsible for the difference in affinity with which successive portions of Rb-ions are bound, as judged from the complex character of the absorption curve? For the moment, any answers to these and similar questions would merely be speculation about the properties of a system for whose existence any more direct evidence is lacking. The same consideration holds with respect to the inflection points. Do the carriers occur in different structural states in the sense that one state having a fixed binding capacity is stable within a certain range of ion concentrations but breaks up into a different structural arrangement with a higher binding capacity when the external concentration of the ion is raised?

The hypothesis that the alkali cation carrier is a molecular structure rather than some simple chemical compound, fits in with the conclusion drawn in the preceding paragraph that binding sites similar to those involved in alkali cation transport are not at all rare in the cell. The representation of the carrier as some mysterious chemical compound with unique properties, seems hardly reconcilable with a protoplasmatic concentration of identical or at least closely related substances as high as 0.1 M. It looks rather as though common cell components are involved, whose structural capacities for specific binding of ions as prevailing in the living cell, however, have not yet been fully disclosed. Recently, Wiggins (1964) described a selective accumulation of K-ions by rat kidney slices, for which she holds the cell proteins responsible. Tempting though this assumption may be for our system too, because of the considerable evidence for a close linkage between ion transport and protein synthesis obtained from work with antibiotics, the direct proof of the nature of the molecular structure involved remains a challenge to further experimentation.

Emphasis on the importance of protoplasmatic structure in ion absorption dates back to 1957, when Overstreet put forward the view that the ion carrier is the living protoplast itself, of whose complicated and labile structure the ions absorbed are – either permanently or temporarily – going to make up an integral part. It is this view to which, in our opinion, the data presented lend support.

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THE HOMOLOGY CONCEPT IN PHYTOMORPHOLOGY—SOME MOOT POINTS

A. D. J. MEEUSE

(*Hugo de Vries Laboratory, University of Amsterdam*)

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ABSTRACT

1. Various aspects of the homology concept are critically discussed, including (*a*) the difference between the scholastic or 'classical' basis of the concept and the neomorphological (phylogenetic) or 'dynamic' approach, (*b*) the requisite of a reciprocity of the relationships among homologous elements belonging to the same conventional (i.e., a static and intranscendent) organ category, (*c*) the relativity of the homology concept in phylogenetic botany, and (*d*) the necessity of recognising categories of *ab initio* inhomologous objects other than those distinguished in static morphylogy (i.e., essentially, the postulation of *organa sui generis* — already silently practised in traditional morphological thought — along different lines).

2. Irrespective of the question whether the neological, i.e., evolutionary and hence 'dynamic', approach to the problem of homology is conceptually and methodologically different from the conventional, i.e., typological and 'static', phytomorphology, the conclusion must be drawn that the two are, in several respects, incompatible, the reasons underlying the differences in some fundamental acceptances and the ensuing interpretations being (*a*) the different delimitations of the intranscendent categories of morphological units (organs, etc.), (*b*) the invariable and 'all or none' equivalence of morphological entities in static phytomorphology *versus* the relativity of the homology relation in the 'dynamic' (semophyletic) morphology, and (*c*) the restriction of the old tenets of homotopy and homodynamy (serial homology) in the New Morphology by the additional requisite of constancy of organogenetic and histogenetic induction during the ontogenetic or morphogenetic differentiation and development of the organs and other structures involved.

3. A consequent application of the neomorphological principles leads to the rejection of several mainstays of the conventional interpretative morphology, such as the 'sporophyll' (foliar carpel and phyllomic stamen) concept, and also to the emendation, or the dismissal, of several allegedly phylogenetic deductions and conclusions, especially of certain aspects of the Telome Theory (in the form developed by Zimmermann).

4. The application of the homology concept to organs belonging to the same individual, and to organs differentiating during diverse phases in the life cycle of an individual (such as the alternating gametophytic and sporophytic generations, or the vegetative shoot development and the state of flowering), also involving the concepts of homotopy and homodynamy, is discussed and the limitations in the application of the concept are outlined against the background of genetic potential, phenotypic expression, determination, induction and morphogenetic differentiation.

5. The comparatively insignificant contribution of teratology to interpretative morphology is explained.

1. STATEMENT OF THE PROBLEM

Recently a paper on the homology problem was published (ECKARDT, 1964) in which once more the statement is made (l.c., p. 81) that there is only one premise underlying all homology concepts, notwithstanding the rather dissentient views expressed by several other workers (see, e.g., SIMPSON, 1961, p. 78–79; BOCK, 1963). The controversy may appear to be rather trifling, but there are some fundamental questions which compel me to challenge the generalisation in Professor Eckardt's paper. This criticism concerns what I hold to be the most essential differences between the so-called New Morphology (N.M.) and the conventional phytomorphology (Morphology 'Old Style', M.O.S.). Surprisingly, even most neologists failed to recognise these differences.

The principal bone of contention can be expressed in the form of the following question: – Is a homology concept which is based on the phylogenetic principle of 'common origin' (of 'propinquity of descent'), and is defined accordingly, different from the traditional (O.S.) homology concept which is based on the vague typological tenet of 'essential structural similarity'? Eckardt and others, such as BOYDEN (1947) and REMANE (1954), believe that the answer must be in the negative because the 'phylogenetic' definition of a homology relation is, in their opinion, primarily based on typology and, hence, only conventional morphology in disguise. However, I agree in so far with Simpson and Bock that there are certain differences between the two interpretations of the homology concept, if not in principles or philosophies, at least in a number of details and in certain applications, so that the alternative approach may lead to some altogether different deductions. It is, in my opinion, irrelevant whether this different outcome is attributable to a different insight into the proper method of approach to certain scientific problems, or rather to a different system of logic. P. SMIT (1964) has – most convincingly, I think – shown that the influence of the early nineteenth century school of 'natural philosophy' on German biological thought is still manifest, especially in the field of comparative morphology. There are also positive indications that in some continental 'schools' morphological thinking is still based on the 'idealistic' phytomorphology, sometimes interwoven with thomistic ideas. I may not be the most competent judge of trends in cognition theory and in phenomenology, but it strikes me that quite often the morphological and phylogenetic conclusions of one phytomorphological school are alleged to be deduced by a process of circular reasoning by protagonists of a different school of thought. Frequently this is a matter of the pot calling the kettle black, so that attempts to reconcile the different points of view will prove to be a thankless undertaking. The present paper is an effort to bring certain rather neglected aspects of the homology concept to the fore which may, I hope, clarify some points and thus contribute towards a better understanding of the controversy. It is up to the reader to decide whether the traditionalists' points of view concerning the theory of homology needs extension or modification, as I believe it does, in the light of neomorphological principles, but in any event the controversial issues must clearly be singled out as a starting point for future discussions before we may hope to gain a better understanding of this corner stone of biomorphology.

2. SOME SEMANTIC ASPECTS OF THE HOMOLOGY CONCEPT

Eckardt has again stressed the, in some circles at least, apparently still prevailing notion that morphology is the study of the unity of diversity by referring certain forms (shapes) or structures to a common reference pattern or 'Gestalt': "*Morphologie ist also Bauplanforschung oder Typologie*" (ECKARDT, 1964, p. 79). He refers to the conventional ways of expressing homology, such as Owen's definition of homologous entities as objects exhibiting 'essential structural similarity', and Darwin's 'correspondence of the organisation plan' (see also BOYDEN, 1947), but like so many before him, does not touch upon – let alone concede – the largely subjective element in the selection of the common item of reference for a group of homologous objects (a so-called 'natural' group, or a specified organ occurring in such a natural group), i.e., of the structural pattern on the basis of which that group is supposed to be modelled (*casu quo*, to have been created). The delimitation of the 'natural' groups is completely aprioristic and not infrequently such a group is 'defined' as an assembly of organisms *having* the same basic pattern (the same 'essential' structure, also referred to as 'archetype', 'prototype', '*Bauplan*', 'structural plan', 'fundamental organisation', 'architecture', or by another term for what is essentially a kind of blueprint). It is quite clear that, at least theoretically, such a basic 'blueprint' or theme (idea!) can serve as a starting point for a number of 'expressions' or 'realisations' of that same structural organisation plan, so that all variations on this same theme have a common denominator of a sort and, as a group, are also automatically different from all assemblies of other (*essentially* dissimilar) objects whose structural qualities are modelled according to a different standard pattern. Conversely, a definition of a natural group as an assembly of entities or specimens whose morphology corresponds with the same essential *Bauplan* can be given. However, the crux of the matter is that the various categories of homologous objects (the 'natural' groups) are preconceived, either directly, or implicitly by their (postulated!) common standard of reference. It is often claimed that comparative morphology supplies the best proof of the existence of a common *Bauplan* by showing, within the natural groups, graded series of transitions 'linking' all variants of the same pattern semi-continuously. This is of course also a case of circularity of deduction (and of wishful thinking), because the group was already preconceived as an assembly of specimens 'belonging together' (on account of what else but an intuitively assessed structural similarity?). In phytomorphology O.S., the morphological organ categories (the 'natural' groups of homologous entities) have, in addition, a very strong bias on account of the M.O.S. being markedly 'Angiosperm-centred', so that not more than three organ categories are aprioristically recognised, viz., the, in the Angiosperms upon the whole rather conspicuously distinct, groups of 'stems', of 'roots' and of 'leaves'. All subsequent attempts to 'demonstrate' that these three types of organs (or two, if one is inclined to combine 'stems' and 'roots' and to distinguish them as 'axial' elements from the 'appendicular' phyllomes) are essentially and entirely diverse things are likewise examples of circularity of reasoning.

That a tendril is sometimes a modified leaf (or a part thereof), but sometimes represents a modified stem-piece or a whole shoot, is universally accepted, and, similarly, the equivalence of the spines or thorns with different organs (leaves, leaflets, stipules, or axial organs) is clearly understood, although in these cases the phenetic resemblance between the inhomologous objects is particularly striking. This rather patently gives away the starting point of the morphological classification, viz., the aprioristic assumption that there *exists* a limited number of morphological organ classes, each category or group embracing homologous elements, and the different groups morphologically dissimilar or inhomologous elements. The recognition of this scholastic foundation of the conventional homology concept simplifies matters considerably. In Eckardt's recent paper under discussion its author devotes an appreciable amount of space to the presupposed similarity of essential structure, i.e., the community of the basic or intrinsic *Gestalt* of the morphological pattern (or *Bauplan*, etc.) of homologous objects, whilst completely evading the issue of *how to decide* (in any other way but by intuition, that is) if two morphological entities have the same 'essential' quality that renders them equivalent. This decision is always biased, the common point of reference alone being already preconceived! Once the, traditionally opposed and mutually exclusive, morphological categories have been postulated, one can only judge subjectively in which of these intransient groups a certain organ fits best. However, in a number of cases this has deteriorated into a conventionalism or even into complete hearsay. The literature on the interpretative morphology of what is called the angiospermous 'flower', especially of its gynoecial ('carpellary') elements, keeps piling up, but if a worker *starts* from the assumption that all Angiosperms have flowers conformable to one and the same structural pattern (*Bauplan*, etc.) which represents a modified leafy shoot, and that all their genitalia are essentially modified leaves or aggregates of such leaves, all his subsequent deductions aiming at a confirmation of the 'classical' floral theory, i.e., of such *postulations* as the foliar nature of the carpels, are inconclusive because they follow from a process of circular reasoning. There is not much point in trying to 'prove' what has already been taken for granted and has in point of fact been the starting point of the discussion (see also UNRUH, 1939, and the forthcoming thesis by my collaborator Moeliono).

So ingrained had the recognition of the three traditional organ categories become in phytomorphological thinking that these concepts were 'extrapolated' into the morphology of the Lower Cormophyta by assessing and interpreting the nature of their organs in the rigid terminology of the Angiosperm-centred classification of organs as 'stems' and 'leaves' (as cauline *versus* foliar, or as axial *versus* appendicular). BREMEKAMP (1962, p. 28) criticised this unwarranted generalisation by saying, when referring to the 'sporophyll' doctrine, that outside a taxonomic group certain concepts may be completely meaningless and in any event require a relativation of their scope. Somewhat similar ideas were expressed by MASON (1957). It is, therefore, in the first place the static and intolerantly rigid classification in

P.O.S. that must be critised. In this system there was scarcely any room for such important structures as thecae, ovules, integuments, funicles, arils, pseudoarils (arillodes), etc. Indeed, the thecae and the ovules (with their accessory organs) were rather generally considered to be merely portions of a fertile appendicular organ (a 'sporophyll', 'foliar carpel', etc.) and, phytomorphologically speaking, hardly of any consequence – so much so that Eames (1961, p. 283–285) discusses the morphological nature of the ovule as if this so essential structure were only an 'emergence', an epidermal outgrowth of the 'carpel', which is of course totally absurd, the advent of the foliar element, in this train of thought, preceding the emergence of the ovule (in other words, prior to the phylogenetic appearance of the ovule sexual reproduction must have been non-existent!). The precursors of the essential ovular structures (called nucellus, integuments and funicle), i.e., the megasporangia and their stalks, are of course undeniably 'older' than the carpels (Meeuse, 1963a, 1964).

Equally vexatious to traditionalists are the implications of the thrusting of this rigid morphological classification (O.S.) upon the telomic *Eocormophyta*.

Returning to the foundations of the homology concept, we must replace all previous attempts of a practical definition of 'homology' by beginning our analysis with the rather trivial and non-committal statement that homology, in the most general sense of the word, is a relation which provides a criterion that can serve to distinguish categories of living beings, or of parts of organisms, from dissimilar categories. In other words, two or more of these objects are associated in some way or another by something they have in common or by an equivalent relation of each of them to a common standard of reference, to a common denominator of a sort, and are thus different from all other objects with which they have none such characteristic features in common or do not share a common denominator. This is a prerequisite that is valid irrespective of all other aspects of the definition of homology. It does not make any difference either, if the objects are only *reputed* to be similar or dissimilar.

It should be noted at once that the relation between homologous entities, as here defined, is not necessarily, and quite often not by a long shot, in the nature of a perfect or 'true' identity. Here lies a possible cause of an adulteration of the concept. When Eames (1961, p. 218) refers to "*. . . the classical view that the carpel is a fertile lateral appendage of a determinate stem tip*", and continues: "*In details of position and origin on the stem, and of ontogeny and anatomy, it is like the leaf and is clearly of leaf rank. Comparative studies of the stamens . . . show that this sporophyl . . . is, like the carpel, basically leaflike in form, structure and ontogeny*", it is not quite clear if he means that a carpel or a stamen is, strictly speaking, a leaf homologue in a classical sense. It all depends on a possible difference in *nuance* between the terms 'of leaf rank' or 'leaf like' and 'homologous with a leaf' ('a true leaf homologue'), i.e., the *equivalent* of a vegetative phyllome or trophophyll, or something more (or less) than that. Such a semantic vagueness and ambiguity is most unsatisfactory and I shall discuss this point again later on.

If the above-mentioned first approximation of a circumscription of 'homology' (and inhomology!) applies to every form and to every notion of homology – as indeed it does in my opinion – one could maintain that conceptually there can only be one form of homology relation, which could be interpreted as meaning that there is no fundamental difference between a phylogenetically defined homology and one based on typology. However, and this is of vital importance, although its semantic basis seems to be sound the given definition is hopelessly inadequate in that it falls short of our goal, i.e., of what we really intend to convey, namely the correspondence of essential features and, more particularly, of *correlated* essential characters. Let us look at some examples. If two or more plants that are so different that they indubitably belong to different taxa bear flowers with red petals, they form for this reason a group of plants which is undoubtedly different and hence distinguishable from all other assemblies of angiosperms that have petals of a different colour. Although these forms share a 'common' character (the red petals) and are distinguishable as a group, presumably not a single phytomorphologist would, on this evidence alone, consider the flowers of these plants to be homologous entities as opposed to (and hence inhomologous with) all flowers that have petals of a different colour. This is not surprising, because the homology concept O.S. is concerned with structural features, not with 'non-essential' colours. However, if the red colour is brought about by the presence of a pigment of a rather unique chemical composition, the picture may change considerably – Bock (1963) and others, including the present author, extend the homology concept to include equivalence of other characters than the structural ones alone, such as a correspondence in chemical composition, in physiology, in behaviour, etc.

Let us now replace the colour character by a numerical difference in the spatial arrangement: if a flower is tetramerous, this does not mean that the flower is *per se* only homologous with tetramerous flowers and not with penta- or trimerous ones. Still, the consistent occurrence of tri- or pentamery is usually considered to be indicative of a 'natural' group (as opposed to other groups with a different number of members in each whorl, cf. Monocots and Dicots). Apparently there are borderline cases, and a homology relation can also be 'relative' in respect of other homology relations (see also Bock, 1963).

A second restriction is introduced by the assumption that a certain feature occurring in taxa which do not constitute a 'natural' group ("do not possess the same essential architecture", M.O.S.), or are phylogenetically unrelated (N.M.), is not necessarily homologous throughout these taxa, but may, on account of a 'superficial' structural resemblance, only simulate homology. Such cases are considered to be examples of analogy, homoplasy, convergence, parallelism, or (Bock, 1963) 'evolutionary homodynamy'. However, this reasoning is biased because the supposed degrees of relationship of the various taxa are, up to a point at least, also preconceived, and chiefly based on the very same features that are supposed to be homologous (or inhomologous, as the case may be). From a theoretical point of view, at any rate, such instances (and forms) of inhomology can be assumed to exist (and there is indeed enough circumstantial evidence to corroborate this assumption in a number of examples). It follows that a close structural resemblance suggesting a morphological equivalence, or even an identity (compare the examples of the diverse morphological categories of tendrils and thorns), is not invariably indicative of homology.

On the other hand, there are examples of a relation which is more than a mere homology. The leaves of one branch of a tree are, for all practical purposes, identical objects (replicates, like the coins minted from the same mould) and it seems unduly formal to call them 'homologous', because they are all phenotypic expressions of the same genome. The same reasoning applies to all leaves of an individual tree and, generally speaking, also to the leaves of all individuals of the same botanical species (they having approximately the same genome), but is it still applicable to the trophophylls of all individual members of a natural taxon of a higher category? I think the answer to this last question must be in the negative, in the first place because phenotypic manifestations of the diverse genomes of not so closely allied species can hardly be expected to be identical replicates, and this applies *a forteriori* to taxa of a higher rank. In addition, the principle of serial homology is at issue, which, in the higher plants with their 'open' type of growth by means of vegetation points, is not necessarily of the same nature as serial homology in animal groups with an 'overall' development of the body (with a 'closed' type of growth). This point has been discussed by the author in a somewhat different context (see MEEUSE, 1963b) and will be dealt with again presently. It can be stated in anticipation that a distinction of homology *versus* inhomology is not just a matter of strictly opposed and mutually exclusive categories, but also depends on other relations which in-introduce a *relative* character into the homology concept (see also MASON, 1957).

When the conventional definition of homology is now reconsidered, the best provisional general circumscription seems to be: "*A relationship based on common characteristics or on a common item of reference, which relation must be restricted primarily to structural features and is used to refer an object to an aprioristically recognised group (or category) in a morphological classification; a second restriction to be made is that homology is not usually a more or less perfect identity, and, conversely, a striking structural similarity is not necessarily indicative of a high degree of morphological equivalence*".

3. THE SUI GENERIS CONCEPT, OR THE PRINCIPLE OF 'EITHER – OR'

In phytomorphology O.S. one starts from the assumption that there is a limited number of different and mutually exclusive, 'static' and 'rigid' categories of elements constituting the plant body. This is clearly a case of 'either – or', i.e., an organ is either a leaf, or a stem or root, and it can not be both a leaf *and* a stem (or root). It is sometimes disguised as a 'bud', but since a bud is a prospective shoot one has, ultimately, to fall back on these same categories. According to BREMEKAMP (1962), the concept of *organa sui generis* has not been very popular in the classical plant morphology, but he, like so many others, overlooked the fact that the postulation of alternative and invariable categories implicitly presupposes the *sui generis* nature of each category in respect of the other ones. This oversight is understandable, because up to now nearly everybody only considered (and usually rejected) the possible *sui generis* origin of the fertile organs in respect of the vegetative ones, although most workers silently accepted the *sui generis* nature of the three 'fundamentally different' organ categories in respect of one another, or at least of two mutually exclusive and intransient categories of 'axial' *versus* 'appendicular' elements.

In the conventional system of morphological classification there is no room for anything else but the recognised categories: an organ is either the one thing or the other. However, if – as is customary in the N.M. – the paleobotanic evidence is taken into account, one of the first fundamental results emanating from the neomorphological approach is the conclusion that the consequent application of the morphological tenets O.S. to fossil plants leads to inconsistencies, which demonstrates the inadequacy of at least some of the classical dicta in phylogenetic botany. The principle of 'either – or' fails when it is applied to the morphology of the Eocormophyta in the conventional way: the psilophytic rod-like vascularised pieces of differentiated thallus, called telomes (and mesomes) at the proposal of ZIMMERMANN (see his latest compilation of the Telome Theory, 1965), can not be referred to the stem or to the leaf category (or to the root class, for that matter) because they constitute, in all probability, the precursors of both the foliar and the cauline organs. The 'either – or' principle that seems to be so neatly applicable to the leaves and stems of higher plants (more precisely: of the Angiosperms!), is inadequate at the early phylogenetic level of the Psilophytes. In other words, the leaves and the stems of the spermatophytic forms, as having a common pattern of reference (a common origin), are not primarily *sui generis* in respect of each other. According to the general definition of homology given on p. 457, they must be homologous entities. Following in Zimmermann's footsteps, several protagonists of neological ideas have extended the 'classical' dicta by interpreting all organs as more or less modified syntelomes, i.e., as more or less derived aggregates of the same basic units, the telomes (including mesomes, as the case may be, but this is a mere technicality). This is essentially what STEWART (1964) dubbed the 'Upward Look' in phytomorphology. By postulating the equivalence (homology) of all telomes, irrespective of the presence or the absence of terminal sporangia, the Telome Theory supplied a tentative explanation of the 'long established' and reputedly fundamental homology of all foliar (phyllomic, lateral, or appendicular) organs: aggregates of telomes which underwent planation and webbing became phyllomes, whereas the remaining telomes (and mesomes), after certain modifications, acquired an 'axial' (cauline) nature. However modern the Telome Theory may seem to be, in this respect very few essential changes took place in basic phytomorphological thought, the same three organ categories still being recognised as those distinguished in plant morphology O.S. The mainstay of the classical or ranalian floral theory, the postulate of the foliar or appendicular character of the genitalia of the Flowering Plants, was thus 'saved', notwithstanding the fact that seemingly the principle of 'either – or' was abandoned. However, the whole deduction hinges on one very fundamental premise, namely on the equivalence of the so-called 'sterile telomes' and their counterparts, the 'fertile telomes' in Zimmermann's terminology, and we are again confronted with the possible *sui generis* origin of certain elements. ZIMMERMANN (1964, 1965) has joined issue with the present author on account of the latter's opinion (MEEUSE, 1963a, p. 132–9) that the cormophytic sporangium is *sui generis* in respect of the vegetative organs of the sporophyte, so that the homology of a 'fertile telome' with a 'sterile' one is restricted to its vegetative portion or sporangiophore and does not include the terminal sporangium. This controversy is, properly speaking, intimately associated with the phylogenetic origin of the terrestrial plants (MEEUSE, 1966b). The connexion between this problem and the mutually *sui generis* nature of the sporangia and the sporangiophores (telomes) will be discussed presently. Suffice it to say that Bower's frequently quoted aphorism: "*The sporangium is older than the leaf*" can be modified into: "*The sporangium is older than the telome*". It goes without saying that something which is phylogenetically older than a different element can not possibly be a subordinate and integral part of that other element, because it had already originated before the second came into being. The fact that such 'ready-made' structures as sporangia and sporangial homologues (such as ovules) are not infrequently secondarily *incorporated* in a more complex organ also containing elements with some foliar characteristics (such as pteridospermous fronds) does not alter the fact that they are not of the same derivation as the elements with the phyllomic nature and are beyond the homology relations of the *vegetative* associated elements. In other words, sporangia and derivatives of sporangia can not be discussed in terms of 'leaves' and 'stems', because they are antipodal, being *sui generis* in respect of the latter. Therefore, the deductions following from a phylogenetic approach to the homology concept do not seem to be very different from those obtaining in morphology O.S. in that the principle of 'either – or' (the *sui generis* nature of certain, mutually exclusive, categories) applies in both instances. The definition of homology requires the stipulation that homology is restricted to organs which are not mutually exclusive (*sui generis*) in respect of one another, organs (and other entities) of independent origin being inhomologous by definition. However, the dividing line between the principal groups of inhomologous categories must be drawn in a completely different place, the phylogenetic approach indicating the fundamental difference between the truly fertile organs and the essentially vegetative parts of the sporophyte, instead of the semophyletically false, conventional categories of caulomes and phyllomes. In the conventional morphological classification of organs there was no 'room' for any other organ but a 'leaf', a 'stem', or a 'root', so that the interpretation of tegumentary envelopes of the megasporangium homologue did not usually go beyond an assumed equivalence of the integuments with indusia (epidermal outgrowths) or with parts (lobes) of a sporophyll, and the whole ovule was sometimes compared with a bud (i.e., with an incipient shoot).

The greater freedom of interpretation provided by the recognition of these *a priori* distinguished categories of vegetative *versus* fertile organs permits the conception of certain truly phylogenetic hypotheses such as Benson's explanation of the origin of one of the spermatophytic ovular integuments as a modified soral or synangial aggregate of megasporangia (see MEEUSE, 1963a, 1964).

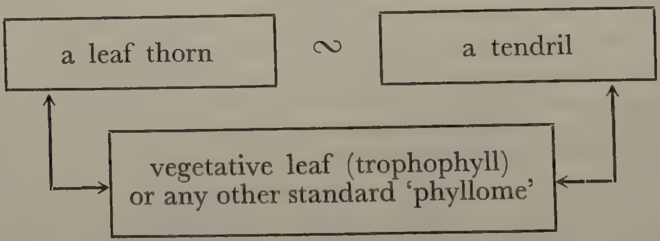
Another implication of the homology concept is the requisite of the reciprocity of the relation between homologous objects, to be discussed in the following chapter.

4. THE RECIPROCITY OF THE HOMOLOGY RELATION

The homology concept in the mathematical sense relates two homologous quantities through their connexions with a third. The homology of two quantities a and b can be expressed as follows:

$$a \backsim b, \text{ but also as } b \backsim a,$$

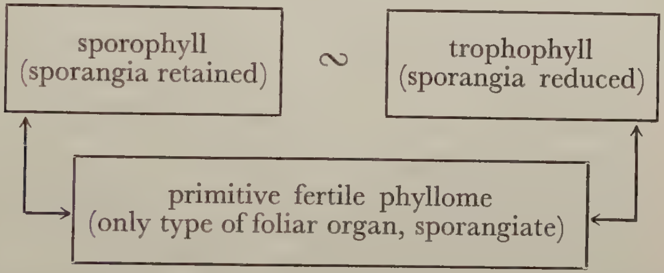
i.e., the relation is reciprocal. In phytomorphology, the reciprocity in the relation between homologous organs has not received sufficient attention, perhaps because one was wont to judge the various elements in an assembly of homologous entities by a common standard of reference (the 'essential structure', 'type', 'basic pattern', *Bauplan*, etc.) the mutual morphological equivalence of the elements of an assembly being underrated. The recognition of certain categories (leaf, stem, root) implies that homologues are reciprocally related, if only indirectly through the 'common standard of reference', thus, for instance:


a leaf thorn
∾
a tendril
vegetative leaf (trophophyll)
or any other standard 'phyllome'

Apparently the requisite of reciprocity does not cause any difficulties in this case. The relation between thorn and phyllome being very much the same as that between the phyllome and the tendril, the equivalence of thorn and tendril is rather obvious. The general validity of this rule of reciprocity permits its application to all cases of an assumed homology relation. However, if we symbolically render the traditional homology relation between vegetative leaves (trophophylls) and fertile floral appendages as follows:

trophophyll ∾ sporophyll,

this relation seems to be somewhat suspect if it is indeed reciprocal, although it is merely a different expression of the fundamental homology relation on which the whole 'classical' interpretation of the angiospermous flower rests. The logical conclusion was drawn by Unruh (1939), who, by means of a purely conventional deduction, decided that the more 'primitive' and phylogenetically 'older' type of appendicular organ is the fertile phyllome or 'sporophyll', because the reciprocity implies that, within the limits of standard morphological thought, the trophophylls can conceivably only be derived from fertile appendicular organs by the loss of the sporogenous elements (the thecae or ovules) of the latter. Unruh expressed this unequivocally by calling the vegetative leaves *Vergrünungen* (virescences) of the fertile phyllomes, in other words, the trophophylls are supposed to be derived from (and phylogenetically younger than) the sporophylls. In diagram:


sporophyll
(sporangia retained)
∾
trophophyll
(sporangia reduced)
primitive fertile phyllome
(only type of foliar organ, sporangiate)

The reciprocity of a homology relation, properly speaking, only obtains in static systems and, therefore, has only a limited scope in the N.M. as we shall see. Still, it can be used to demonstrate certain inconsistencies. Apart from the example of an atavistic development of the fertile brachyblast of *Ginkgo biloba* I have already discussed elsewhere (see Fig. 1, adapted from Meeuse, 1966a), the supposed morphological identity of a sterile telome and a fertile one advocated by Zimmermann (e.g., 1959, 1964, 1965) is a case in point. The reciprocity of the homology of the two categories of telomes causes some complications. Quite apart from such questions as homotypy, morphogenesis, determination and differentiation to be discussed presently, the phylogenetic consideration that the sporangium is most probably 'older' than the intercalated vegetative sporophyte (the sporangiophore) and *sui generis* in respect of the latter (Meeuse, 1966b), is already at variance with the reciprocity of the relation which implies that an organ bearing a terminal sporangium is, or was, equivalent to a similar structure devoid of such a sporuliferous extension. The so-called sterile telome can only be equivalant to as

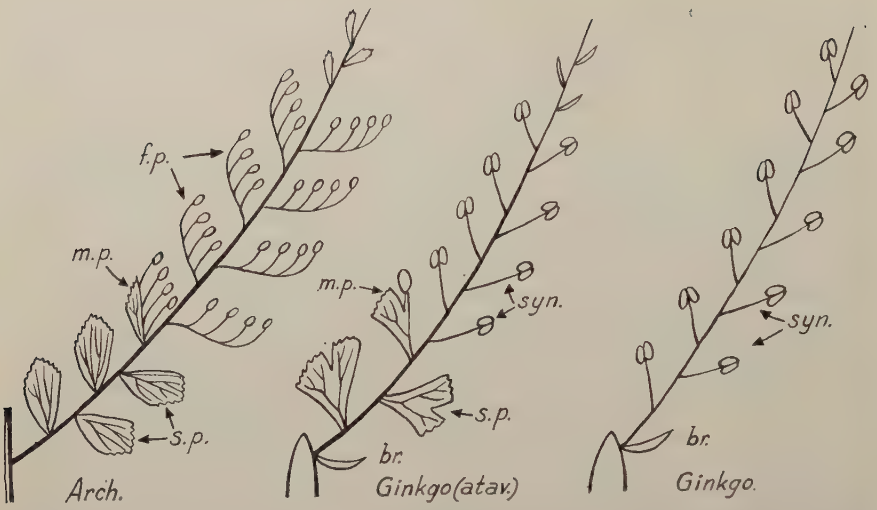


Fig. 1. Atavistically developed male brachyblast of *Ginkgo biloba* (centre) which is reminiscent of a putative progymnospermous archetype more or less closely corresponding with a fertile pinna of an *Archaeopteris* frond (*Arch.*, left). Right: a normal male brachyblast of *Ginkgo*. All figures diagrammatic; *s.p.* sterile pinnule; *f.p.*: fertile pinnule; *m.p.*: mixed pinnule (an additive, not necessarily a partly substitutive aggregate of 'sterile' and 'fertile' telomes, and hence *not* unequivocally indicative of the equivalence = homology of adjacent fertile and sterile portions); *syn.*: stalked synangia; *br.*: axillant bract of brachyblast.

fertile one without its sporangium. Even if one assumes that a 'sterile' telome may conceivably be derived from a 'fertile' one by the loss of the sporangium, the homology is not 'complete' because the reciprocity is no longer 'complete' after the reduction of an essential integral part of one of the homologous subjects and can only extend as far as the limits of the 'retained' elements, thus excluding the (altogether dissimilar) reduced portion (in the case under discussion, the sporangium). It was on the ground of very similar, logical deductions that Unruh reached his paradoxical conclusion concerning the origin of the trophophylls as we have seen.

As a yardstick of morphological equivalence, the reciprocity is very important in various contexts. According to the telome theory, an aggregate of associated telomic elements, a syntelome, can evolve into an organ of the leaf class, or differentiate into an organ of cauline nature, depending on the morphogenetic processes operative during its semophylesis from a number of more or less independent telomes to an integrated organ of a more complex structure. It would follow from the postulated equivalence of fertile and sterile telomes that a syntelome compounded of sterile telomes that became a 'stem' must still be homologous with a derivative of a sporangiate syntelome of the phyllome class. Zimmermann only considered the cases of an aggregate of sterile telomes constituting a vegetative ('sterile') syntelome that became a trophophyll, and its counterpart, the mixed syntelome built up of sterile and fertile telomes that he supposed to have become a leafy 'sporophyll'. However, the principal difference between such structures as the proto-coniferous fertile brachyblasts and the supposed fertile phyllomes or sporophylls of the Cycadopsid groups, usually considered to represent entities belonging to the mutually exclusive classes of cauline (or axial) and foliar (or appendicular) organs, respectively, is not at all attributable to the origin of the two fertile structures under discussion from aggregates of fertile and sterile telomes, but to different morphogenetic processes. The divergent, phenotypic modifications evolved gradually during the phylogeny and the semophylesis of each group and they had no bearing on the initial homology relation that existed between the elementary telomic elements incorporated in the syntelomes, i.e., on the primary equivalence of these elements. A coniferous female brachyblast originated as an aggregate of sterile and fertile telomes which eventually fused to form the ovuliferous cone scale that is subtended by the bract scale and can for that reason not be referred to the phyllome class, although it is the phylogenetic derivative of a mixed syntelome that underwent some webbing just like the cycadopsid fertile pterophyll or sporophyll is supposed to be in Zimmermann's interpretation of its semophylesis. In Zimmermann's own publications other derivatives of complexes of sterile and fertile telomes than the coniferous cone scales are referred to the category of the appendicular organs and named (appendicular) 'sporophylls'. Clearly the original morphological equivalence between the telomic and syntelomic precursors of fertile organs does not provide an adequate criterion to assess the homology of these organs at a much higher level of organisation. The evolutionary derivatives of identical archetypes acquired the 'special quality' of a phyllome or of a cauline organ, respectively, i.e., of one of two categories of traditionally antipodal elements. This is manifestly the result of the semophyletic advent of morphogenetic processes which progressively differentiated the appendicular organs from the axial ones. Somewhat surprisingly, this obvious conclusion still does not unequivocally explain why, at the present-day level, a certain type of fertile organ (viz., the ovuliferous cone scale), is, by a fairly general consensus of opinion, referred to as a fertile brachyblast, whereas the so-called megasporophylls of the Cycadopsid forms are supposed to be appendicular leaf homologues, although, according to the telome theory, the same elementary processes (in this case planation and webbing preceded or followed by some overtopping) are responsible for the semophyletic changes in shape and position. The supposition made by Zimmermann, and repeated by several other telomists, that, when an aggregate of fertile and sterile telomes (a mixed syntelome) and a corresponding vegetative syntelome evolved into a laminose structure, the fundamental identity of the telomes and the syntelomes is maintained, i.e., that the phylogenetic homology of sphorophylls and trophophylls rests upon a morphological equivalence of the archetypes persisting during the series of evolutionary changes in morphogenesis (and organogenesis in the proper sense) to which their derivatives were subjected, is clearly untenable. Irrespective of the answer to the question whether the so-called fertile telomes are complete homologues of the sterile ones, the morphological equivalence of the 'sporophylls' and the trophophylls of the Spermatophyta rests exclusively on the degree of similarity of the elementary determinative processes to which the supposedly identical archetypes were subjected during their evolution. The morphology of the fossil progymnosperms strongly suggests to me (see MEEUSE, 1963a) that the vegetative (and assimilatory) laminose organs of their descendants developed exclusively from 'sterile' syntelomes by the advent of morphogenetic processes which included planation and webbing, whereas the sporangiate complex syntelomes forming the complex, partly fertile and partly sterile ('mixed') frond-like structures of the proto-spermatophytes initially evolved without a previous association of the sterile and the fertile telomes into integrated units that subsequently behaved as single semophyletic entities, and without a process of webbing involving the fertile pinnules of these 'mixed' fronds. A subsequent *secondary* incorporation of derivatives of the fertile elements (such as ovules) in, or an adnation to, already laminose ('phyllomic') structures does not necessarily imply that the resulting laminose derivatives (so-called 'sporophylls' of, e.g., seedferns) are *per se* the morphological equivalents of the trophophylls. Their different mode of origin would rather preclude the unequivocal homology of the sterile assimilatory elements (leaves, trophophylls, vegetative fronds, etc.) and the fertile pseudo-sporophylls. The fact that the fertile phyllomes of many true (isosporous) ferns may well have originated in the fashion suggested in Zimmermann's Telome Theory (i.e., as a mixed syntelome during the semophylesis of which both the sterile and the fertile elements of the soma of the progenitor partook in the process of webbing) has no bearing on the problem under discussion, because there is sufficient evidence to accept an independent evolution of the fern and seed plant lineages. A secondary cladodification of non-foliar elements during the phylogeny of an organ is equally irrelevant in this respect.

The principle of reciprocity obviously can not be applied to the ultimate stages of the dynamic semophyletic sequences belonging to divergent evolutionary lines, unless one relates the conformity of essential structure by a comparison at the phylogenetic level of the common prototype. The, at the onset of their evolution, reciprocally homologous entities have each acquired a special character determined neither by the morphology of the archetype (which is a telomic structure in any event), nor by the fundamental organogenetic processes operative at the telomic and post-telomic levels of organisation, but by the sequence, the interaction, and the relative time of initiation of these processes. These determinative changes have a considerable bearing on the relative degree of homology obtaining between originally equivalent and subsequently modified structures as shall be explained in the following chapter. For the time being it suffices to point out that the shifting degree of morphological similarity is conceptually incongruous in the static phytomorphology Old Style.

5. THE RELATIVITY OF THE PHYLOGENETIC HOMOLOGY CONCEPT

Definitions of homology, i.e., of a morphological equivalence, based on a common origin (on a propinquity of descent from a common prototype) as given by SIMPSON (1961) and by others, are inadequate as we have seen, because a divergent semophyletic evolution may mould originally identical structures into derivatives belonging to different morphological categories of organs (e.g., into axial elements or into phyllomes). The comparison of the secondarily inhomologous entities at various evolutionary levels yields different results depending on the semophyletic phase of differentation, in other words, on the relative time factor. At the early phylogenetic stage of the dichotomously branched telomic Eocormophyta there was no clear distinction between 'axial' and 'appendicular' organs before the process of overtopping became manifest: every telome and every mesome occupied the same relative position in respect of its supporting mesome, viz., a 'semi-terminal' one. Leaving the sporangia out of consideration, we may accept that all telomes (and mesomes), and, accordingly, all vegetative syntelomes, are homologous structures. It was only after a process of overtopping that the 'lateral' position of some of the elements (viz., the overtopped ones) in respect of the overtopping ones became recognisable. Similarly, the processes of aggregation, planation, and webbing may each in their turn have caused a differentation of the various elements, but normally two or more of these morphogenetic and determinative processes operated simultaneously. The same cumulative effect of the diverse morphogenetic processes on a number of homologous archetypes need not necessarily have altered the homology of the derivatives of the latter appreciably. However, a different sequence or intensity of these processes, but especially a different degree of interaction, may conceivably result in a progressively diminishing degree of morphological equivalence of the semophyletic derivatives of initially identical structures. The relation between morphological structures (or other organic entities, such as taxa, for that matter) is apparently dependent on various factors which – in phylogenetic botany at least – render the homology a *relative* quality. Thus a trophophyll is the homologue, by direct semophyletic derivation, of an aggregate of telomes, but a stem supporting the trophophyll, although also a derivative of a corresponding aggregate of telomes, is no longer the equivalent of the trophophyll even if their respective ancestral stages were fully homologous. At the present phylogenetic level of clearly distinct trophophylls and axes (caulomes) these organ categories are certainly not homologous if judged by the three criteria of the classical morphology again brought to the fore by ECKARDT (1964): they differ markedly in their mode of origin (in their ontogeny and morphogenesis), in their structural (anatomical) pattern, and in their 'special quality' (of an assimilatory appendicular organ and a supporting and translocating cauline organ, respectively). Yet they had propinquity of descent and consequently a certain degree of homology must still be attributable to them on account of their common origin from telomic structures. The phylogenetic level of comparison and the common point of reference apparently matter a great deal in the assessment of the homology or inhomology of certain structures. The correspondence in the structural pattern and other indications of an initial morphological equivalence may ultimately diminish to such a low level that examples of inhomology rather than of homology seem to be present. This relativity of the homology relation is of far-reaching importance in connexion with the interpretative morphology of the reproductive structures of the Spermatophyta. After a clear differentiation of telomic aggregates into sporangiate (fertile) non-laminose structures and into overtopped laminose vegetative appendages of the rhachis of the compound (mixed) fronds of the progymnosperms (see, e.g., the latest reconstruction of *Archaeopteris* by Beck, 1962), the original homology of syntelomes had already been altered because they had attained semophyletic phases exhibiting a manifest lack of correspondence. The overtopped vegetative phyllome-like elements (the vegetative 'pinnules') are, at least functionally, already trophophylls and have acquired a lateral or appendicular position in respect of the supporting non-laminose organ which thus became promoted to the rank of a 'leaf-bearing' axis (and, in point of fact, soon assumed some of the characteristics of a spermatophytic cauline element, for instance a secondary growth in girth as observed in the 'petiolar' and main rhachidic axes of the progymnospermous 'fronds').

Insofar as the fossil records are trustworthy, we may assume that in the progymnosperms and in the seed ferns the sporangiophores (the sporangium-bearing telomes) did not *ab initio* become incorporated in a laminose overtopped appendage of a rhachidic axis (a so-called sterile pinnule) of the compound frond because they were during their early evolution apparently not subjected to a determinative morphogenetic induction process causing planation and webbing. On the contrary, the coalescence of the telomic elements of the so-called fertile pinnules of the progymnospermous and early pteridospermous fronds took the form of longitudinal mutual adnation of the sporangiophores which thus became a stalk-like synangiophore that did not exhibit a single singular characteristic of a phyllome (Meeuse, 1963a). A subsequent coalescence and webbing of telomic axes to form a cupule around the ovule initiated *after* a clear differentiation into sterile pinnules (formed by a process of planation followed by webbing, semophyletically evident from various phases found in such forms as *Svalbardia* and *Archaeopteris*, see Fig. 2) and fertile pinnules (formed without a manifest process of planation followed by webbing, and apparently having lost their original assimilatory function) is a case of independent origin of the cupule as a third, i.e., neither strictly foliar nor manifestly cauline, category of sterile organs. The, phylogenetically speaking, still more recent incorporation of derivatives of the fertile pinnules (ovules and their stalks) in a

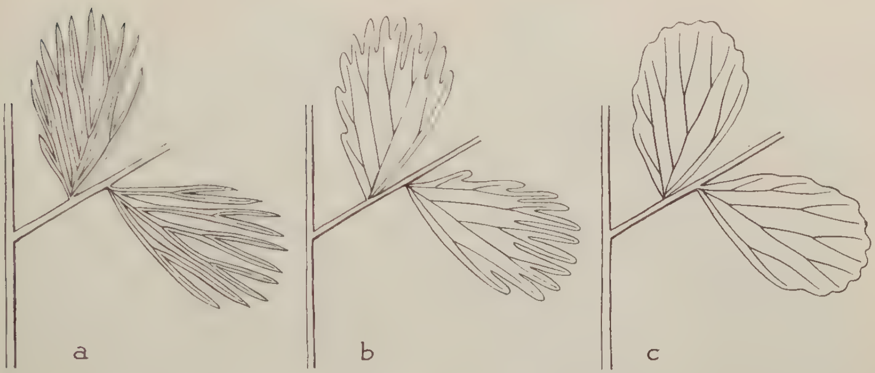


Fig. 2. Three stages of the semophylesis of a sterile progymnospermous pinnule, as illustrated by portions of the (sterile) fronds of different form species of *Archaeopteris*. A repeatedly bifurcate and assimilatory syntelome (protophyllome) *a*, already lateral in respect of the supporting protocaulome (rhachis), and also known from such fossils as *Svalbardia*, evolves into a 'simple' leaflet or pinnule *c* (also known from the fronds of, e.g., sphenopterid Pteridosperms) by a process of 'webbing', *b* representing an intermediate stage. It is assumed that the planation had already occurred before the initial phase *a*.

laminose structure as a result of the progressive increase of the surface area of the laminae of the assimilatory leaflets of 'mixed' pteridospermous fronds (the derivatives of the vegetative pinnae of their archetypes) does not make the already cupule-borne ovules leaf-borne after the event (see Fig. 3).

The various structures under discussion – the vegetative leaflets of phyllomic nature, the stems and other 'axes' such as the petiolar frond stalk and the rhachis, the ovular stalks, cupules and male synangiophores – all originated as syntelomes, but soon evolved along different and divergent lines. The homology of the various organs was, (if we disregard the sporangia and the sporangial homologues) reciprocal and absolute at the level of the undifferentiated syntelome, but the relation became progressively more obscure as each category of organ evolved along its own semophyletic pathway of evolution. The relative degree of homology is best illustrated by the interpretation of the nature of the cupule. After its initiation as a branched, more or less 'cage-like' syntelome a process of webbing occurred which transformed its rather loosely associated component parts into a close-knit and continuous, cup-shaped or campanulate to urceolate structure and in this respect it differs from stems and from synangiophores (which were not subjected to a process of webbing), so that one might consider a cupule to be more leaf-like than a truly cauline organ such as a stem, a root, or a pteridospermous petiole or frond rhachis. On the other hand, a cupule is undoubtedly less leaf-like, i.e., of a more cauline nature, than a trophophyll. This reasoning involves the 'special quality' of each organ category and, therefore, can not altogether be separated from the respective functions of the organ. Soon the cupule followed its own evolutionary pathway and

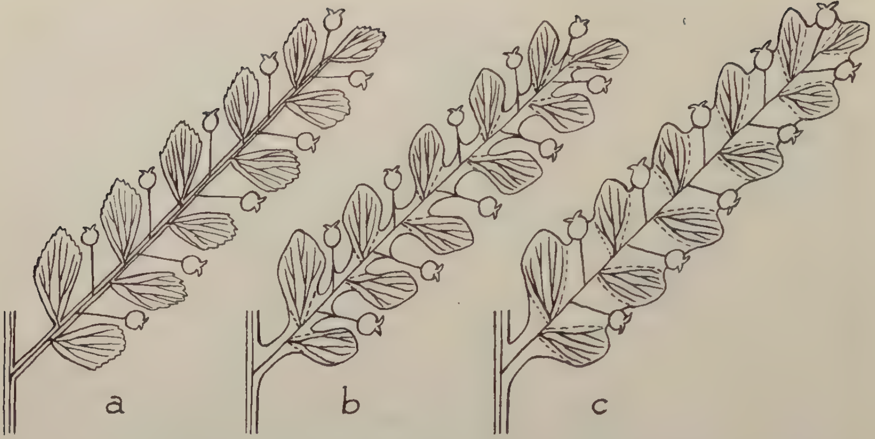


Fig. 3. The 'simplification' of a fertile pinna of a pteridospermous frond, diagrammatic. In the initial phase (*a*) the sterile pinnules are still primitive in that they have a cuneate base (compare also Fig. 1*a* and Fig. 2). By the lateral extension of the assimilatory (phyllomic) leaflets (*b*, *c*.) the 'laminae' of these pinnules join to form the assimilatory portions of a single simple pinna which has incorporated the stalks of the coaxial fertile organs (e.g., ovules, cupules). The resulting leaf-like structure bearing 'marginal' ovules (or cupules, etc.) is not a true 'sporophyll', but a secondarily originated aggregate formed by coalescence and adnation *after* the initial segregation of telomic archetypes into laminose protophyllomic structures (the vegetative pinnules) and non-laminose, non-photosynthetic (protocauline) elements (synangiophores, rhachides of fertile pinnules) had been completed.

its interpretation as a cauline (axial) or a foliar (appendicular) organ becomes inane – it is neither stem nor leaf but a derivative of a syntelome that independently developed its own 'special qualities'. The ovules of the cycadopsid groups, primarily inserted on organs of cupular derivation, can not be considered to be axis-borne (and the *Cycadopsida*, accordingly, not truly stachyosporous), but they are not really leaf-borne (and the *Cycadopsida*, therefore, not phyllosporous) either.

The relativity of the homology relation was previously sensed and had already been expressed in several different ways. Bremekamp was quoted before as saying that 'outside' a certain group (or taxon) the relation called homology has only a limited scope and that it may loose its original meaning if one extends its application to other groups than the one it was established in originally. At an earlier date, Mason (1947) had discussed a relativity within and between morphological classes of organs such as exists among elements of the floral envelopes (perianth lobes, tepals, sepals, petals), prophylls, bracteoles, bracts, trophophylls, phyllomes, etc., and their respective derivatives such as foliar thorns and tendrils, elements reduced to glands, bud scales, etc. The degree of morphological equivalence (or homology) between elements *within* each subordinate group (in the example given, belonging to the phyllome class) need not necessarily equal the degree of correspondence existing between elements belonging to *different* groups. As Mason clearly points out, the assessment of morphological equivalence depends to a large extent upon the relation of the entities to be compared (or assessed) with other entities or groups of entities: a sepal corresponds better with another sepal of the same whorl than with a petal of the same flower, although they both belong to the phyllome class of floral appendages; in other words, the similarity, and hence homology, is relative. BOCK (1963), as we have seen, attributes a great deal of importance to the various forms and degrees of inhomology and pseudo-homology, a subject dealt with by the present author in a somewhat different fashion under the heading '*Lines and Levels*' (MEEUSE, 1966b, Ch. 8). The assessment of degrees of homology, of homoplasy, of parallelisms, of 'evolutionary homodynamy', etc., is largely decided by 'relative' yardsticks such as the geological time factor and the comparison in the semo-phyletic sequence (in a 'line') as opposed to a comparison of different 'lines' at the same time 'level'. The shorter the time interval, the closer the correspondence between the elements of the 'lines' and the 'levels' in a group showing radiating evolution, so that Bock has rightly pleaded for a restricted assessment of morphological relationships by applying our standards of judgment only to smaller 'natural' groups of taxa (BOCK, 1963, p. 283: "*Homology is not an absolute quality but varies just as much as monophyly.*"). This does not imply that one could not pursue semophyletic studies, but one should not base one's deductions on the Angiosperm-centred terminology and semantics of the classical morphology (In Bock's terminology: One should beware of silently accepting a transcendence outside the categories!). In several recent text-books and in other publications the anatomical features of, e.g., a pteridospermous frond rhachis are used as if they were indicative of the nature of the organ involved by being assessed at the 'level' of the higher cycadopsids. The once-pinnate and simple leaf-types of the higher cycadopsid groups are the semophyletic derivatives of the complex fronds of protogymnospermous and pteridospermous archetypes. The principal rhachidic axes of these complex fronds were structures which can perhaps best be called 'protocauline', but in the cycadopsid line of descent they eventually became subordinate elements (the principal veins) of a discrete entity, the simple bennettitalean, chlamydospermous and angiospermous 'leaf'. The 'same' protocauline organs developed, in another evolutionary lineage, into the axial portion of the ginkgopsid and coniferopsid 'leafy shoots' and they assumed all the characteristics of a stem including radial symmetry and secondary growth. The assimilatory appendages of these coniferopsid shoots and of the twigs of *Ginkgo* are functionally trophophylls, hence 'leaves' of a sort, but they are not the homologues of an angiospermous simple leaf which incorporates in its lamina a number of elements each of which is the homologue of a coniferopsid trophophyll. This is another demonstration of the relativity of the homology concept when applied in a phylogenetic sense.

Summarising the arguments, I believe one can safely assume that the relativity of the homology relation is the most essential difference between phytomorphology O.S. and the N.M. as regards the interpretation and the semantics of the concept of homology.

6. MORPHOLOGICAL RELATIONS BETWEEN ORGANS OF A SINGLE INDIVIDUAL AND RELATED CASES

The morphological relationships between different portions of the same organism, of topologically corresponding parts of individuals belonging to the same taxon of lower rank, and of the two generations of the same taxon (gametophyte and sporophyte), have been discussed in terms of 'determination', 'differentiation', 'morphogenesis (histogenesis)', 'correspondence in development (in ontogeny)', 'serial homology', 'equivalence through homotopy', etc. These terms are sometimes more or less contradictory and in any event the whole picture is rather confusing, because frequently only one aspect is emphasised in a series of deductions and the other aspects are conveniently left unconsidered (see also MEEUSE, 1963). ZIMMERMANN (1964, 1965) among others, defends the complete morphological equivalence (hence: homology) of the fertile and sterile telomes, by basing their equivalence on their common origin from the same single element. For example, an apex of a telome axis may divide longitudinally to produce two prospective daughter telomes. If one of these division products develops into a sterile telome and its twin counterpart into a sporangiophore topped by a sporangium (a so-called fertile telome), the reasoning followed by Zimmermann is that the two elements originate in the same way, viz., as perfectly identical ('twin') derivatives of a single entity and retain this identity (apparently irrespective of any subsequent differences in ontogenetic and histogenetic development). This train of thought is not so easily applicable to the more complicated situations found in, e.g., the shoot apex of a spermatophytic plant which in its most apical part is undoubtedly a single and self-perpetuating entity, but whose tunica differentiates in the somewhat older regions into entirely different things, viz., into the future stem cortex and the leaf primordia. Obviously a different organisation is induced by some morphogenetically active principle or by a gradient of such a determinant. I fail to see why this is not the *general* case when organs develop, and prefer to explain the process of a different ontogenetic and histogenetic organisation in initially identical structures as the resultants of different morphogenetic inductions acting upon the same substratum. This explanation still holds if this supposition is applied to the extreme case of the single fertilised egg cell: out of a single entity, the zygote, a complicated organism develops comprising several types of organs, tissues, cells, etc., although in principle the genetic constitution (and hence the genetic potential) is retained in the nuclei of all derivative cells of that fertilised egg cell. Apparently the genetic factors responsible for the changes and the differences can only express themselves in certain preconditioned regions or zones and sometimes, as in the case of sporulation or flowering, only after an initial period of growth and development of some duration and not infrequently after an additional induction. There must be a remarkable interaction between the genetic code and the responding regions of the organism which moulds seemingly equivalent things, such as groups of practically identical cells, into diverse structures that are by general consensus of opinion nominally inhomologous after their maturation. The assessment of homology exclusively based on a common origin from morphologically equivalent ontogenetic (precursory) stages is, therefore, often manifestly false. In an earlier paper (Meeuse, 1963) I have already suggested that only if organs (or other, comparable structures), develop in the 'same' (i.e., corresponding or homotopic) places in the same sequence and histogenetically in exactly the same way can there be a morphological identity. If the histogenetic (or 'ontogenetic') development of more or less clearly homotopic organs (e.g., serially originating elements) does not follow the same pattern and, as can frequently experimentally be ascertained, it is regulated by other morphogenetic forces than those previously operative, e.g., by the introduction or translocation of various quantities of biochemically active substances (which are usually restricted in their action to certain areas, zones or 'fields', or produce gradients to which the substratum responds only locally), there is not necessarily a high degree of morphological correspondence between these organs of unequal ontogeny (and of unequal '*Gestalt*' and anatomy in the mature stage). The genetic potential is essentially present in all nucleate cells, even among higher plants the 'latently' omnipotent somatic cells often betraying their potentialities in cases of regeneration (also in tissue cultures!), of adventitious bud formation (e.g., along the leaf margins of species of *Kalanchoë*, etc.), of wound healing and of artificially induced abnormalities. Out of cells of an organ belonging to a fixed category, say, a phyllome (such as epidermal cells of a *Begonia* leaf), an entire shoot (bud) may develop which contains an axial organ belonging to an altogether different class of organs. Nevertheless we maintain the distinction between cauline and appendicular organs because of the manifest differences in *Gestalt*, in structure, in histogenesis, in function, etc. in their mature state. In other words, one of the old criteria of homology, a corresponding ontogenetic development, should be emended to read (in addition to other requisites of homology): "*and a conformity of morphogenetic determination*". The principle of serial homology, and also of some other forms of homotopy, is only applicable with this restriction. The traditional, alleged equivalence of all floral appendages, of the sterile as well as the fertile ones, is chiefly based on this principle of serial homology (i.e., of homotypy combined with a supposed similarity in development). However, the mere fact that in several cases the change-over from the vegetative phase of the shoot apex to the reproductive condition only initiates after some florigenic stimulus (for instance, an appropriate sequence of photoperiods) has acted upon that apex, knocks the bottom out of the argument, the induction causing a different determination associated with differences in the histogenetic development resulting in a different adult structure and '*Gestalt*'. Similarly, sporulation and gametogenesis in lower cormophytic forms only set in at a certain developmental stage. Presumably such processes are also governed by the interplay of genetic potential, various morphogenetic inductions and the structure, symmetry and polarity of the somatic substratum or the growing parts thereof. The fact that a gametophytic generation succeeds a sporophytic one, and *vice versa*, is genetically determined it is true, but regulated by the interaction of a number of factors. The homology (*casu quo*, inhomology) of the gametophytic and the sporophytic generations of the same species is pertinent to the question of the origin of the early terrestrial plants (for a discussion, see MEEUSE, 1966b). In the 'homologous' theory concerning the advent of the eocormophytes, the two alternating generations are supposed to be isomorphic, whereas in the alternative 'intercalation theory' the gametophyte and the sporophyte are supposed to be *ab initio* different ('antithetic'). Being an adherent to the second hypothesis, I believe that also in this example one should attempt to distinguish between genetic potential, phenetic 'Gestalt' (i.e., the phenotypic expression of these potentials) and determinative morphogenetic processes as much as possible. There is a certain plasticity, which is also a demonstration of the genotypic potential. The wel-lknown experiments with mosses in which vegetatively propagated sporophytic tissue develops into a diploid gametophyte and other examples of the 'transcendence' (or 'spilling-over') of sporophytic characteristics to the gametophyte, such as the occasional occurrence of tracheids in the prothalli of *Psilotum*, show that there is a certain amount of flexibility. The incidental transcendence of features of one stage may become phylogenetically stabilised, as has, for instance, happened in the primary xylem of certain Dicotyledons which contains pitted tracheary elements reminiscent of secondary xylem cells and quite unlike the typical tracheids of the primary xylem (which have ring-shaped, reticulate, or helical wall thickenings). This is an example of 'adult' features having become precocious, but the opposite, viz., the persistence of characteristics of the younger developmental stages (in other words: proterogenesis or neoteny) is presumably also of frequent occurrence. The importance of neoteny during the evolution of the higher Spermatophyta has for instance repeatedly been advocated in the writings of the Armeno-Russian botanist TAKHTAJAN (1959a, 1959b).

In bryophytic and pteridophytic forms, the different gross morphology, anatomy and ecology (physiology) of the gametophytic and the corresponding sporophytic generation is clearly the result of a different morphogenetic determination. In accordance with my previous conclusion concerning serial homology, the different histogenetic induction in the prothallus and in the sporophyte points to the inhomology rather than to the homology of the haplontic and diplontic phases. The postulation of isomorphic alternating generations in the progenitors of the archegoniate land plants is clearly incongruous in respect of the conditions in the living cormophytic forms, but even if this is left aside it is not pertinent to the question of homology or inhomology of certain structures. Organs that were identical at an early phylogenetic stage may have undergone so many changes during a subsequent divergent semophyletic evolution that they are no longer equivalent as we have seen, so that initially isomorphic haplontic and diplontic generations (or parts there of) need not remain homologous after a divergent evolution. The early hemicormophytes transitional between green algae and archegoniate plants did, in my opinion, not have an alternation of independent isomorphic generations and the vegetative parts of the sporophyte presumably arose *de novo* (i.e., *sui generis* in respect of the gametophyte and of the sporangia). There is, accordingly, and irrespective of their ontogenetic and histogenetic origin, no homology between the gametophytic soma and the sporophyte, nor is there an equivalence between a sterile telome (a part of the vegetative sporophytic soma) and a so-called fertile telome (a part of the vegetative soma plus the inhomologous sporangium). As we have seen in one of the previous chapters, such simple and clear-cut assumptions pave the way towards a neological approach to the dynamic phytomorphology of the higher Cormophyta and to the phylogenetic ('relative') homology concept.

7. Teratological aspects

Teratology had always been considered to be indicative of the morphological nature of the malformations, or at least to have some bearing on their interpretative morphology, until Heslop-Harrison (1952) made it very clear, in my opinion, that one should distinguish two forms of abnormal development, viz., (*a*) the truly atavistic terata which are manifestations of the genetic constitution of ancestral forms by a recombination of genetic factors through which certain retained 'ancient' genes (alleles) which normally are not phenotypically expressed, regain their capacity of a phenotypic expression, and (*b*) the various deformations resulting from abnormalities in the rate of growth and differentation during development caused by an interfering (stimulating, inhibiting, selectively distorting, etc.) influence throwing the processes of histogenesis and organogenesis out of gear. Examples of the first group are such phenomena as the development of a fertile fifth median stamen in quadristaminate zygomorphic flowers of *Scrophulariaceae* and *Labiatae*, the presence of an additional stamen (or of two) in the flowers of *Orchis* and *Dactylorchis*, and the occasional development of a pistil instead of the pistillode in (secondarily) unisexual flowers, the occurrence of three or more microsporangia in a stalked synangium in the male *Ginkgo* instead of two, etc. Upon the whole such cases are clear and unequivocal. Examples of the second category are again of two kinds, the one being only an abnormal development of the vegetative soma, and the other being more complicated by an abnormal sex expression. Sex determination and sex expression have been the subject of several papers by Heslop-

HARRISON (e.g., 1957). Aberrant forms of sex expression are almost invariably a substitution of one sex by the other, i.e., a 'reversal' of the sex expression in equivalent (homologous) structures (see also MEEUSE, 1965, Ch. IX, p. 95–111). Atavistic abnormalities are, generally speaking, so clear-cut that they are anything but exciting, and, accordingly, the morphological interpretation is in most instances evident from a comparative analysis (see, e.g., the 'series' *Verbascum*, with 5 stamens → *Celsia*, with 4 and a staminode → *Scrophularia*, with 4 → *Veronica*, with only two developed stamens: the homotopy of a staminode or nectary with a 'missing' stamen already betrays its nature). Deformities caused by an aberrant growth rate and/or an irregular differentiation do not usually have much demonstrative force in the interpretative morphology of the floral region: a phyllodic 'degeneration' of a pistil, even if concomitant with virescence, is not an unequivocal proof of the foliar (appendicular) character of a 'carpel' (MEEUSE, 1963b). Sex reversal must be interpreted as an interchange of male and female (micro- and megasporangiate) structures and this may be a guide in the analysis, whilst it may serve as an aid in avoiding errors of judgment. The partial difference in sex expression in, e.g., a female coniferous cone (a so-called androgynous one) or in an amentiferous 'catkin' should not be morphologically assessed on the basis of an equivalence of 'sporophylls' (micro- and megasporophylls, 'carpels' and 'stamens'), but of synangial aggregates, i.e., of anthers and bitegmic ovules. Even such 'problematical' cases as the development of polliniferous, stamen-like structures on the placentae inside an angiospermous ovary (observed, for instance, in *Petunia hybrida* by my Amsterdam colleague, Dr. F. Bianchi) become quite clear if the rules of the interchangeability of the sexes and of the homology of the basic category of fertile organs (the sporangia) are applied: an ovule on its funicle is practically the equivalent of a stamen (of the anther and its stalk, the filament). It is exactly these simplifications which render the analysis rather simple and unambiguous, but at the same time demonstrate the poor value of 'monstrosities' in interpretative morphology. Incidentally, they appear to be more compatible with neological concepts than with the classical tenets.

8. THE CLASSICAL AND THE NEOMORPHOLOGICAL HOMOLOGY CONCEPTS

My starting point was the question whether the conventional homology concept and the pertaining classical doctrines of essential phenetic similarity (homoiomorphy), of correspondence in origin and in development (homotopy, homodynamy, etc.), and of the identity of 'special quality', are not appreciably different from the concepts and the criteria to be applied in dynamic phytomorphology and phylogenetic botany. Protagonists of phytomorphology O.S. have repeatedly accused neologists of assessing relationships between organisms and their integral parts (organs and associated organ complexes) by the same standards as those used in the classical morphology (and conventional taxonomy), followed by a phylogenetic interpretation, or, in other words, of circularity of reasoning. I do not think this can possibly be true, because the basic postulates and the deductions following from these assumptions are not identical with those of the classical phytomorphology. Phylogeny and semophyletic morphology are based on the doctrine of evolution and the first difference between the two concepts of homology is the static classical (and in point of fact scholastic) postulation of fixed and mutually exclusive categories versus the dynamic neomorphology of relative and changing degrees of homology. Bock (1963) clearly appreciates the consequences of the acceptance of the static groups in scholastic thought: *As in the taxonomic tenet of the constancy (non-mutability) of species, morphological categories have absolute boundaries that cannot be transgressed.* Owen's formulations of homology and analogy are based on the philosophy of typological anatomy, i.e., on the postulation of clear-cut 'natural' groups of organisms, each group with a specific and 'ideal' pattern, on the basis of which the morphology of all its members was constructed (or created). Bock also made it very clear that the postulation of homology on a phylogenetic basis rests upon the phylogenetic relationships, i.e., on the relation between various and diverse aspects of organisms and their constituting parts (organs) – including '*Gestalt*' (form), structure (anatomy), function, genetics, karyogenetics, behaviour, ecology, physiology and biochemistry – and that it is something quite different from the working criteria by means of which the (chiefly phenotypic) features are assessed in *practice*, in very much the same way as the theoretical species concept differs altogether from the methods by means of which the practical or 'applied' taxonomist strives at distinguishing ('recognising' !) formal species in his museum or herbarium. The working criteria of applied taxonomy are often inadequate, in my opinion, in that they do not necessarily result in the delimitation and subdivision of a taxon or in the recognition of a semophyletic homology relation which are the only possible ones according to the (admittedly, frequently unknown) evolutionary history of the taxon involved. The standard counter-argument that this distinction is of no practical value whatsoever because the 'theoretical' concept of propinquity of descent cannot be put to the test for the lack of other tangible evidence than the criteria provided by the typological method, is crucial, but, to my mind, not so pertinent as several workers seem to think. If we compare, for instance, the so-called cytotaxonomic approach to the delimitation of species by means of non-conventional (and, in fact, evolutionary) criteria, there is no *a priori* reason to reject a phylogenetic approach of phytomorphology and markedly less so if we consider that the palaeobotanic evidence gathered from numerous fossil records is not meaningless and may be quite consistent. I shall leave it at that as I have discussed this particular point exhaustively elsewhere (Meeuse, 1966a, Ch. II–VI), but I may add that even if one disregards the issue of fundamental method, the neological postulation of intranscendent categories must be altogether different from the conventional one. The gametophyte, the vegetative parts of the sporophyte, and the sporangia are the three basic categories of *sui generis* elements to be distinguished in phylogenetic botany instead of the Angiosperm-centred notions of 'stem', 'root' and 'leaf'. The third difference, apart from the dynamic instead of the static approach and the different delimitation of the fundamental organ categories already mentioned, is the restriction of the criterion of homotopy and serial homology (of the similarity in origin and development) by adding the proviso that this is a reliable yardstick only if the morphogenetic and histogenetic induction is invariable during the various developmental stages or approximately so. These three differences between the Old interpretative Phytomorphology and the N.M. account for quite a few unorthodox interpretations of the organs of the higher *Spermatophyta* and their homology relations given by neologists such as Lam, Melville and the present author (see MEEUSE, 1966a). To sum up, I believe that there are indeed some very fundamental differences, both conceptually and semantically, between the Old Morphology and the New centred around the problem of homology, which inevitably lead to a greater freedom of thought and of interpretation.

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NOTE SUR CALLITRICHE FASSETTII SCHOTSM. NOV. SPEC.

H. D. SCHOTSMAN

(*Centre National de Floristique, Paris*)

(*reçu le 2e décembre, 1965*)

RÉSUMÉ

Cette note comprend la description de *Callitriche fassettii*, nouvelle espèce submergée, appartenant au Groupe I de notre subdivision provisoire du genre (voir SCHOTSMAN, 1966, sous presse). Elle occupe une aire de distribution aux Etats-Unis d'Amérique, dans deux Etats occidentaux qui bordent le Pacifique: l'Oregon et la Californie. La publication traite un point particulier en vue d'une révision complète de « *C. hermaphroditica* ».

Holotypus: no 2746, Oregon's Flora. In small ponds near Dalles City. Wilhelm N. Suksdorf 4.5.1898. L.

DIAGNOSE

Caules filiformes ramosi. Folia ad basin latiora, gradatim attenuata, apice modice profunde et rotunde emarginato, utrinque acumine subulato praedito. Stamen ad 0,7 mm longum, anthera reniformis ad 0,5 mm longa, 0,5 mm lata. Flos femineus breviter pedunculatus, styli ad basin recurvati et plus minusve reversi, parte basali modice crassa, ad 2 mm longi. Fructus pedunculatus, latior quam altus, ad 2,5 mm latus, 1,8 mm altus, saepe e 2 vel 3, raro e 4 mericarpiis; mericarpium insigniter reniforme, modice late alatum, praesertim ad apicem. Cellulae mesocarpii superne visae polygonales, pergentes in alam et ibi praesertim marginem versus multo increscentes magnitudine.

Après nos études sur plusieurs espèces européennes du genre *Callitriche*, nous avons poursuivi nos recherches, notamment sur les taxa aquatiques d'Asie et d'Amérique du Nord.

Ces taxa appartiennent au groupe I de notre subdivision provisoire du genre *Callitriche* (voir SCHOTSMAN, 1966, sous presse).

Dans ce groupe, extension de la section *Pseudo-Callitriche* de HEGELMAIER (1867), nous avons inséré tous les taxa qui croissent complètement submergés.

Voici les caractères principaux du groupe:

Feuilles transparentes, à peu près linéaires, sans tissu lacuneux, sans poils, sans stomates.

Fleurs sans bractéoles.

Etamine dressée avant et après la déhiscence, à anthère incolore dont les parois consistent en cellules parenchymateuses.

Grains de pollen incolores, sans exine.

Poils axillaires composés de 2 cellules basales, surmontées d'un «éventail» à 2–(3) couches de plusieurs cellules.

L'aile des méricarpes, si elle est présente¹), montre les cellules polygonales du mésocarpe.

---

¹) Vue de dessus. Couches externes parenchymateuses enlevées. Chez certaines populations de *C. hermaphroditica L.* les couches externes—plus ou moins coriaces—participent à la formation de l'aile.

Le nombre de base pourrait être $x = 3$: nous avons compté $2n = 6$ sur *C. hermaphroditica* L. (matériel d'Ecosse et du Jardin Botanique de Munich, Allemagne) et sur *C. truncata* Guss. subsp. *occidentalis* Rouy (matériel du Portugal et d'Angleterre).

En Europe, ce groupe est représenté par les espèces suivantes:

1. *C. hermaphroditica* L.
2a. *C. truncata* Guss. subsp. *truncata*
2b. *C. truncata* Guss. subsp. *occidentalis* Rouy
2c. *C. truncata* Guss. subsp. *fimbriata* Schotsm.
3. *C. pulchra* Schotsm. (voir SCHOTSMAN, l.c.)

En ce qui concerne « *C. hermaphroditica* », ce taxon occupe, d'après la littérature (HULTÉN, 1950; FASSETT, 1953), une aire de distribution boréale-circumpolaire.

Or, dans une note antérieure (SCHOTSMAN, 1958), nous avons déjà signalé que « *C. hermaphroditica* » en Europe comprend plusieurs populations distinctes. Une comparaison superficielle des échantillons venant d'Amérique et d'Asie nous a montré nettement que les exemplaires de ces régions, eux non plus, ne sont pas identiques. On peut distinguer des populations ressemblant à certaines populations européennes, mais on trouve aussi des échantillons à caractères très différents.

Il est évident que « l'espèce *C. hermaphroditica* L. » se compose de plusieurs taxa de différentes catégories taxinomiques.

Pour éclaircir le problème, nous avons commencé une révision complète de *C. hermaphroditica*, en comparant soigneusement les échantillons américains, européens et asiatiques.

Dans cette brève note nous exposons un des résultats récemment obtenus en donnant la description d'une espèce nouvelle de l'Amérique du Nord.

Les flores modernes de l'Amérique du Nord, comme celles de FERNALD (1950) et de GLEASON (1958), ne mentionnent qu'un seul représentant de notre groupe I: *C. hermaphroditica* L.[1])

Dans son ouvrage bien connu sur les *Callitriche* du Nouveau Monde, FASSETT (1951), lui non plus, ne fait pas allusion à une autre espèce.

Pourtant, cet auteur a remarqué quelques différences entre les échantillons examinés par lui.

A la page 218, FASSETT dit ceci:

« At first examination there would appear to be two types of fruit on this species. One is broad-winged and plump-sided, ranging from 1.2–2.5 mm in width, while the other is nearly wingless and flat-sided, ranging from 1.0–1.5 mm in width. »

Cependant, le manque de connaissance anatomique plus précise du fruit, d'une part, et d'études comparatives, d'autre part, l'ont empêché de mettre en valeur ses observations. C'est ainsi que Fassett en a tiré, selon notre opinion, une fausse conclusion, en disant (page 218):

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[1]) Nous laissons en attente la nomenclature confuse et ambiguë de JONES et FULLER (1955) et des auteurs plus anciens, comme HOOKER (1834) et TORREY (1843).

« These two types, however, are but two stages in development; the first is found on collections from early June to early September, while the latter is collected from August to December (May, in California). Fig. 24g, then, which can scarcely be distinguished from the fruit of *C. hamulata*, is but an early stage in development. »

Une comparaison de quelques échantillons américains, mentionnés dans la liste des localités de Fassett (p. 215–217) prouve que les « two types of fruit » ne représentent pas deux phases dans le développement d'une seule espèce, *C. hermaphroditica*, mais ils correspondent à des différences taxinomiques réelles et importantes.

Nous reviendrons sur ce sujet dans notre révision complète. Pour l'instant, occupons-nous dans cette note de la description d'un taxon dont quelques échantillons figurent aussi dans la liste de Fassett (l.c. page 217).

Le premier exemplaire de ce *Callitriche* a été trouvé par nous dans l'herbier de Leyde (Pays-Bas). Cet échantillon, venant de Dalles City, Oregon, U.S.A. (Suksdorf, 1898), nous a frappé déjà en 1958 par ses caractères spectaculaires (Schotsman, 1958). Récemment, nous avons examiné deux doubles [2]) qui portent la détermination de Fassett (*C. hermaphroditica* L. – *C. autumnalis* L. Fassett, 1949. F; MO) et, en plus, quelques exemplaires récoltés en Californie dont celui de Kelseyville (MO) a été également vu par Fassett.

Il est curieux que cet auteur n'ait pas discuté, dans son travail, les différences qui existent entre les fruits des plantes de Dalles City et de Kelseyville, d'une part, et le reste des échantillons insérés dans sa liste, d'autre part. La dissemblance pourtant, est très nette: les échantillons de Dalles City et de Kelseyville, contrairement aux autres exemplaires, montrent des fruits pédonculés, plus larges que hauts, à méricarpes réniformes et ailés, caractères par lesquels ce *Callitriche* se rapproche plutôt de *C. truncata* Guss. subsp. *truncata* et surtout de *C. pulchra* Schotsm. que de « *C. hermaphroditica* ».

Or, la sous-espèce *truncata* a été également considérée par Fassett comme *C. hermaphroditica*: l'étiquette sur un échantillon venant de Sardaigne (MO) nous en donne la preuve. On peut en conclure que, d'après Fassett, – qui donc ne tient pas compte de la forme et de la taille des fruits – tous les *Callitriche* à feuilles transparentes appartiennent à *C. hermaphroditica* L.

Revenant sur les *Callitriche* de Dalles City et de Kelseyville, nous estimons, après avoir comparé leurs caractères morphologiques et anatomiques avec ceux des autres taxa du groupe I, qu'il s'agit d'une nouvelle espèce.

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[2]) Fassett a vu plusieurs doubles de ces échantillons. Ces doubles viennent de 4 herbiers américains: GH, MO, CM, US. Nous supposons qu'il y a une petite erreur dans ces abréviations. D'après Fassett (l.c. page 137), « CM » signifie: Chicago Museum of Natural History, mais dans l'Index herbariorum (1956, 3e ed. vol. I; 1964, 5e ed. vol. I), cet herbier figure sous la lettre « F »; en revanche, « CM » correspond à l'herbier de Carnegie Institute, Pittsburgh, Pennsylvanie.

Nous l'avons décrite sous le binôme de *Callitriche fassettii*. Ainsi nous avons voulu rendre hommage à feu NORMAN C. FASSETT (†1954), excellent botaniste, ayant un intérêt profond pour les plantes amphibies et aquatiques.

Ses études taxinomiques sur les *Callitriche*, bien qu'elles ne soient pas basées sur des caractères d'anatomie et de morphologie fine, ont beaucoup contribué à notre connaissance de cette famille critique; sa monographie des taxa américains, surtout en ce qui concerne les espèce terrestres, restera de grande valeur.

Présentons, sans entrer déjà dans tous les détails anatomiques, quelques caractères principaux de *C. fassettii*:

Tiges filiformes ramifiées, 0,3 mm de diam. environ.

Feuilles faiblement soudées à la base, plus larges à la base que vers le sommet, uninervées, longues de ± 12 mm. Echancrure du sommet très profonde, arrondie, à deux apex assez longs et aigus (voir Fig. 1A).

Etamine haute de 0,7 mm, à filet plus court que l'anthère (voir Fig. 1 D, E).

Anthère réniforme, incolore, haute de 0,5 mm, large de 0,5 mm.

Fleurs femelles courtement pédonculées. Stigmates assez épais à la base, réfléchis à la base et plus ou moins recourbés en arrière, jusqu'à 2 mm de longueur (voir Fig. 1 B, C).

Fruit pédonculé (jusqu'à 2 mm), large de 2,5 mm, haut de 1,8 mm, à 4 méricarpes. Quelquefois 1 ou 2 méricarpes avortent (Fig. 2 A).

Méricarpe fortement réniforme, largement ailé. Les méricarpes divergent ou se placent parallèlement. Les sillons dorsiventraux sont très profonds.

Cellules du mésocarpe (vues de dessus) polygonales, à parois tangentielles externes parenchymateuses, à parois tangentielles internes un peu épaissies, de couleur jaune-brûnatre, mais assez transparentes: on voit nettement en-dessous les deux couches de fibres croisées de l'endocarpe. Ces parois internes sont entourées par un anneau lignifié. Les cellules polygonales du mésocarpe se prolongent dans l'aile en devenant très volumineuses, surtout vers le bord. On en compte à peu près 2 rangées à la base du méricarpe et 4 rangées au sommet. Quelques fibres de l'endocarpe se poursuivent dans l'aile (voir Fig. 2 B).

En ce qui concerne la distribution de *C. fassettii*: nous supposons que l'espèce occupe une aire restreinte, aux Etats-Unis d'Amérique, dans quelques Etats occidentaux qui bordent le Pacifique.

D'après les précisions sur les étiquettes, l'espèce pousse dans l'eau courante, mais aussi dans des fossés et des petits étangs.

Nous avons vu les échantillons suivants:

OREGON

In small ponds near Dalles City, 4-5-1898. W. N. Suksdorf. Oregon's Flora 2746. L (Holotype: sub *C. autumnalis* L., non déterminé par Fassett); F, MO

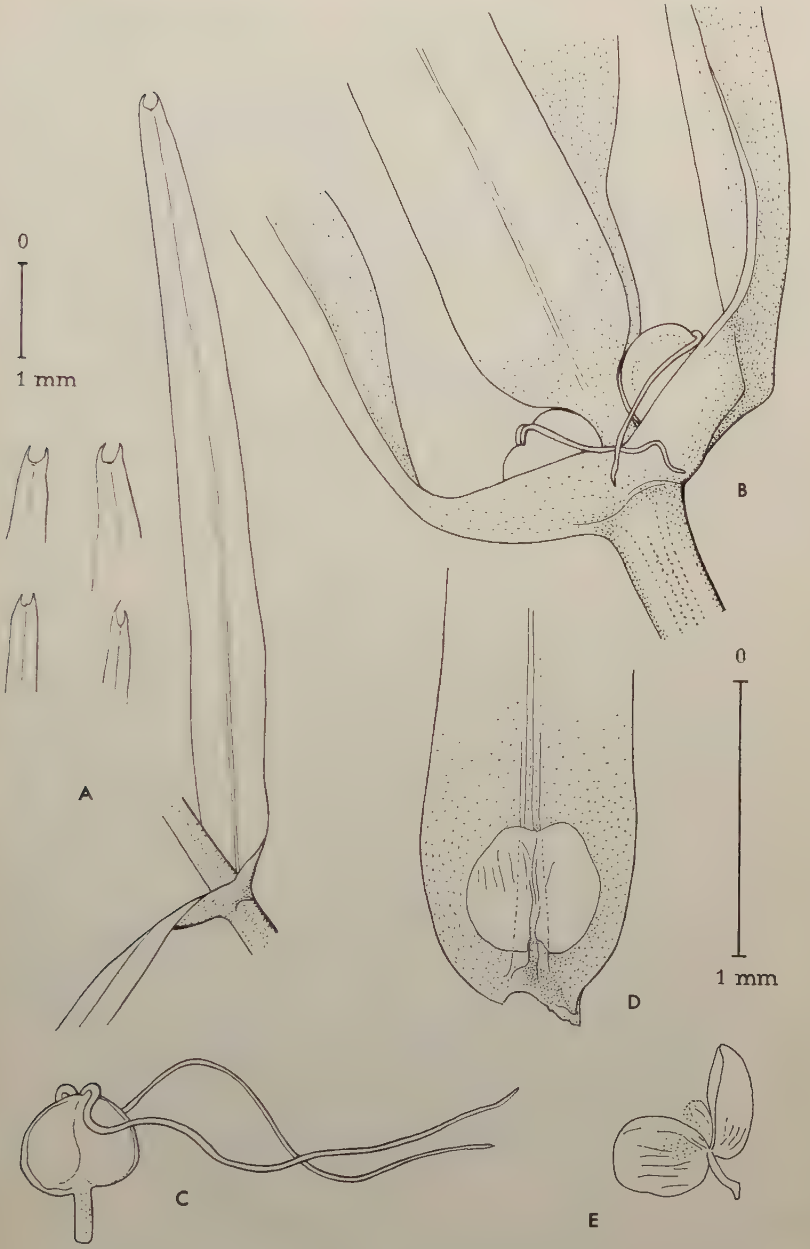

Fig. 1. Callitriche fassettii Schotsm. nov. spec.

A. Feuille et quelques sommets de feuilles.
B. Deux fleurs femelles après la fécondation; stigmates courbés en arrière.
C. Fleur femelle adulte isolée.
D. Partie basale d'une feuille avec fleur mâle.
E. L'étamine après la déhiscence.

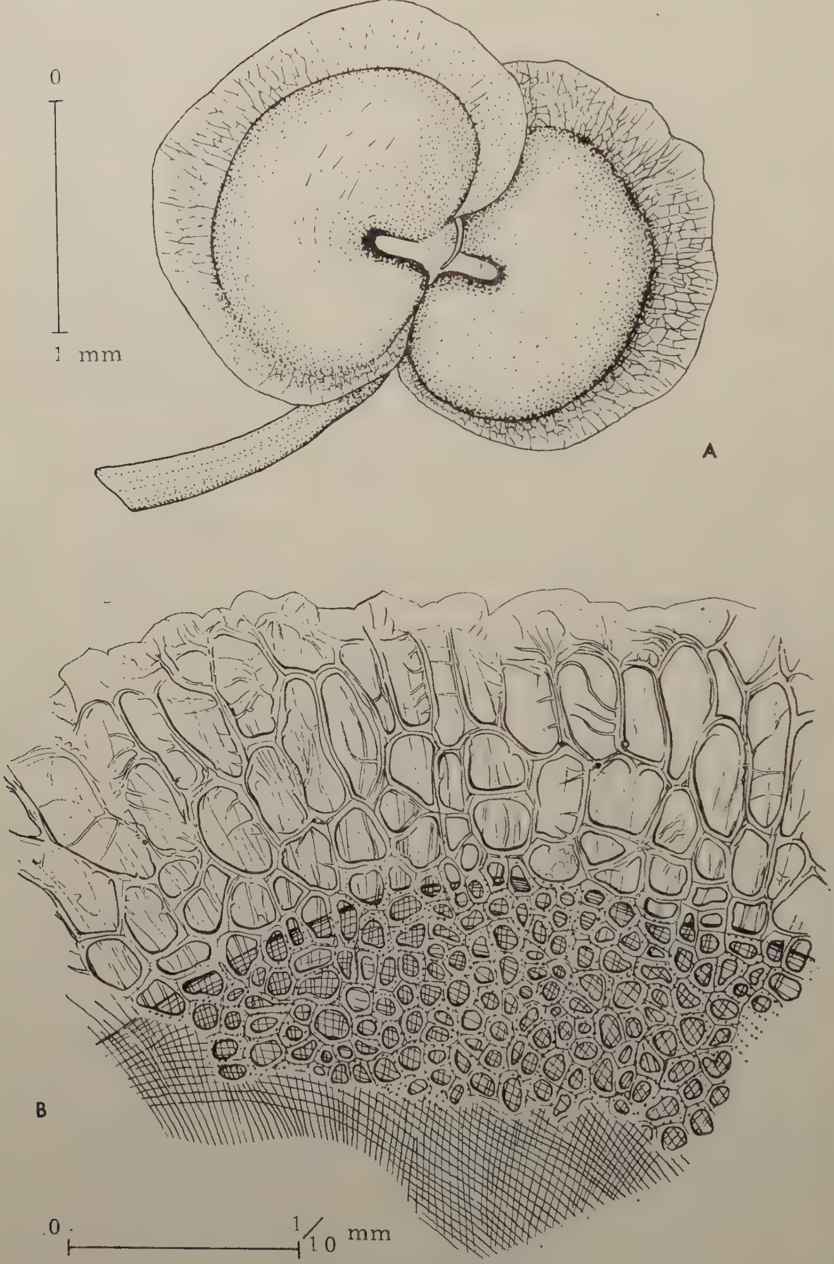

Fig. 2. Callitriche fassettii Schotsm. nov. spec.
A. Fruit à deux méricarpes; vue latérale.
B. Détail anatomique du méricarpe (couches parenchymateuses externes enlevées); vue de dessus.
En bas: cellules polygonales petites de la partie du mésocarpe qui renferme la graine. On voit en-dessous les deux couches croisées de fibres de l'endocarpe.
En haut: cellules volumineuses de l'aile.

(ces deux doubles portent la détermination de Fassett: *C. hermaphroditica* L.—*C. autumnalis* L. Fassett, 1949).

CALIFORNIE

Flora of Lake County, California; *Kelseyville*, 13–5–1929. Coll. by J. W. Blankinship. MO (sub *C. marginata* Torr.; *C. hermaphroditica* L., *C. autumnalis* L. Fassett, 1949).

Dudley Herb. of Stanford Univ. Plants of California 12403; submerged in running streams with *Ranunculus aquatilis*, wooded hills on road to *Friant*, 2 miles south of O'Neil 1), Madera County, 3–4–1951. Roxana S. Ferris and R. Bacigalupi. MO. (sub *C. autumnalis* L.).

Plants of California 13260; entirely submerged in a ditch along *United States Highway* 395, 2.1 miles north-east of *Standish*, Lassen County, 17–6–1958. Peter H. Raven, Otto T. Solbrig. NY (sub *C. hermaphroditica L.*).

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1) Probablement «O'Neals».

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CHROMOSOME NUMBERS OF SOME FLOWERING PLANTS OF SPAIN AND S. FRANCE

TH. W. J. GADELLA, E. KLIPHUIS AND E. A. MENNEGA
(*Botanical Museum and Herbarium, Utrecht*)

(*received September 27th*, 1965)

ABSTRACT

The chromosome numbers of 32 plant species from Spain and S. France, all collected in natural habitats, were determined. Voucher specimens have been deposited in the Utrecht Herbarium.

INTRODUCTION

Very often voucher specimens of cytologically studied plants were not preserved in herbaria. Consequently it is impossible for later investigators to check the chromosome numbers given. For this reason lists of documented chromosome numbers prove to be very useful (cf. the lists published in Madroño and the I.O.P.B. reports published in Taxon). Moreover, in many cases the available information pertains only to the study of one or a few plants of mostly a very limited part of the distribution-area of the species concerned. For these reasons it was decided to study a number of plants, collected in Spain and S. France by Mr. E. A. Mennega during a botanical excursion. Voucher specimens of all the investigated material have been deposited in the Botanical Museum and Herbarium, Utrecht.

MATERIAL AND METHODS

Plants were collected in the form of seed samples or of bulbs. The seeds were germinated, and the seedlings, as well as the bulbs were grown in the Botanical Garden of the State University of Utrecht, "Cantonspark" in Baarn. All identifications were carried out on this material by Mr. E. A. Mennega. At the time of collecting the plants were not in flower. The chromosome counts are based on the study of roottip-mitoses. For this purpose the roottips were fixed in Karpechenko, embedded in paraffin, sectioned at 15 micron and stained according to Heidenhain's haematoxylin method.

RESULTS

The results are given in the following table.

This table gives a summary of the authors' chromosome counts with indication of the origin of the material and a survey of the cytological investigations carried out up to the present.

TABLE

BORAGINACEAE

Cerinthe major L.
coll. no.: 130 . . . . $2n = 16$

origin: Sierra de Carbonera, N. of Gibraltar (prov. of Cadiz)
references:
Britton, D. M. 1951 (Switzerland) . . . . . $2n = 16$

Cerinthe major L. var. *purpurascens* Boiss.
coll. no.: 135 . . . . $2n = 16$
origin: on wall in Tarifa (prov. of Cadiz)

Echium italicum L.
coll. no.: 114 . . . . $2n = 32$
origin: roadside between Lanjaron and Orgiva, S. of Granada (prov. of Granada)
coll. no.: 38 . . . . $2n = 32$
origin: roadside near Sagunto (prov. of Valencia)

Caryophyllaceae

Silene secundiflora Otth
coll. no.: 34 . . . . $2n = 24$
origin: ruins of amphitheatre in Sagunto (prov. of Valencia)

Silene ramosissima Desf.
coll. no.: 139 . . . . $2n = 24$
origin: coastal road W. of Tarifa (prov. of Cadiz)

Tunica prolifera (L.) Scop.
coll. no.: 144 . . . . $2n = 60$
origin: Sierra de Magina, S.E. of Jaen (prov. of Jaen)

Cistaceae

Cistus salvifolius L.
coll. no.: 39 . . . . $2n = 18$
origin: dunes near Albufera, lagoon S. of Valencia (prov. of Valencia)
references:
Chiarugi, A. 1925. (Italy) . . . . $n = 9$
Simonet, M. 1937. (France, Antibes) . . . . . $n = 9$; $2n = 18$
Dansereau, P. 1940. (Medit.) . . . . $n = 9$; $2n = 18$
Bowden, W. M. 1945. (cult.) . . . . $2n = 18$
Atsmon, D. and N. Feinbrun. 1960. (Israel) $2n = 18$
Löve, A. and E. Kjellquist. 1964. (Portugal) $2n = 18$

Helianthemum ledifolium (L.) Willd.
coll. no.: 125 . . . . $2n = 20$
origin: aside coastal road near Estepona (prov. of Malaga)

Compositae

Centaurea polyacantha Willd.
coll. no.: 127 . . . . $2n = 22$
origin: Sierra de Carbonera, N. of Gibraltar (prov. of Cadiz)
references:
Guinochet, M. and J. Foissac 1962. (unknown) . $2n = 22$

Cirsium acarna (L.) Moench
coll. no.: 61 . . . . $2n = 22$
origin: Monte Mongo, near Javea (prov. of Alicante)

Helichrysum stoechas (L.) DC.
coll. no.: 176 . . . . $2n = 28$
origin: dunes near Albufera, lagoon S. of Valencia (prov. of Valencia)
references:
Lorenzo-Andreu, A. and P. Garcia-Sanz. 1950. (Spain) . . . . $2n = 28$

Inula viscosa (L.) Ait.
coll. no.: 3 . . . . $2n = 34$
origin: roadside between Narbonne and Perpignan (S. France)
references:

Rodolico, A. 1933. (Italy) . . . . $n = 9$

Phagnalon rupestre DC.
coll. no.: 8 . . . . $2n = 18$
origin: Castelldefels, S. of Barcelona (prov. of Barcelona)
coll. no.: 26 . . . . $2n = 18$
origin: roadside between Alcalá and Cuevas (prov. of Castellon de la Plana)
coll. no.: 73 . . . . $2n = 18$
origin: steppe near Santa Pola, S. of Alicante (prov. of Alicante)
references:
Larsen, K. 1956. (Italy) . . . . $2n = 18$

Silybum marianum (L.) Gaertn.
coll. no.: 37 . . . . $2n = 34$
origin: roadside near Sagunto (prov. of Valencia)
coll. no.: 118 . . . . $2n = 34$
origin: roadside between Motril and Malaga, near Almuñécar (prov. of Granada)
references:
Heiser, C. B. and T. W. Whitaker. 1948.
(U.S.A., California) . . . . $2n = 34$
Larsen, K. 1956. (Italy) . . . . $2n = 34$
Skalinska, M. *et al.* 1959. (Poland) . . . . . $2n = 34$
Moore, R. J. and C. Frankton. 1962. (cult.) $2n = 34$

Tolpis barbata Gaertn.
coll. no.: 123 . . . . $2n = 18$
origin: coastal road near Marbella (prov. of Malaga)

CRUCIFERAE

Lobularia maritima (L.) Desv.
coll. no.: 10 . . . . $2n = 24$
origin: Castelldefels, S. of Barcelona (prov. of Barcelona)
references:
Larsen, K. 1955. (Italy) . . . . $2n = 24$

Vella annua L.
coll. no.: 74 . . . . $2n = 16$
origin: steppe near Santa Pola, S. of Alicante (prov. of Alicante)
references:
Manton, I. 1932. (cult.) . . . . $2n = 16, 32$

EUPHORBIACEAE

Euphorbia segetalis L.
coll. no.: 28 . . . . $2n = 16$
origin: roadside between Alcalá and Cuevas (prov. of Castellon de la Plana)
references:
Perry, B. A. 1943. (Portugal, cult.) . . . . $2n = 16$

LABIATAE

Salvia verbenaca L.
coll. no.: 5 . . . . $2n = 59$
origin: roadside between Narbonne and Perpignan (S. France)
coll. no.: 21 . . . . $2n = 64$
origin: El puente del diable, N. of Tarragona (prov. of Tarragona)
references:
Benoist, E. 1937. (cult.) . . . . $2n = 54$
Reese, G. 1957. (Algeria) . . . . $2n = 42$

LILIACEAE

Allium polyanthum Bor.
coll. no.: 17 . . . . $2n = 20$
origin: El puente del diable, N. of Tarragona (prov. of Tarragona)

Asphodelus fistulosus L.
coll. no.: 79 . . . . $2n = 28$
79 A . . . . $2n = 28$
79 B . . . . $2n = 28$
origin: steppe near Pola, S. of Alicante (prov. of Alicante)

Dipcadi serotinum Med.
coll. no.: 14 . . . . $2n = 8$, $8 + 1, 16, 16 + 2, 32$
origin: El puente del diable, N. of Tarragona (prov. of Tarragona)
coll. no.: 68 . . . . $2n = 8$, $8 + 1, 8 + 2, 8 + 3, 8 + 4$
origin: Monte Mongo, near Javea (prov. of Alicante)
references:
Levan, A. 1944. (unknown) . . . . $2n = 8$
Fernandes, A. *et al.* 1948. (Portugal) . . . . $2n = 8$
Resende, F. *et al.* 1946. (Portugal) . . . . . $2n = 16$
Reese, G. 1957. (Algeria) . . . . $2n = 64/68$
Chennaveeraiah, M. S. *et al.* 1959. (unknown) $2n = 8$

Lapiedra martinezii Lag.
coll. no.: 60 . . . . $2n = 22$
origin: Monte Mongo, near Javea (prov. of Alicante)
references:
Fernandes, A. 1950. (E. and S.E. Spain) . . $2n = 22$

Muscari comosum (L.) Mill.
coll. no.: 90 . . . . $2n = 18$
origin: roadside between Granada and Sierra Nevada, ± 1200 m (prov. of Granada)
references:
Delaunay, L. N. 1926. (unknown) . . . . . $2n = 18$
Fernandes, A. *et al.* 1948. (Portugal) . . . . $2n = 18$
Larsen, K. 1956. (Italy) . . . . $2n = 18$

Ornithogalum pyramidale L.
coll. no.: 150 . . . . $2n = 16$
origin: Desfiladero de Despeñaperos near St. Elena (prov. of Jaen)
references:
Heitz, E. 1926. (unknown) . . . . $2n = 32$
Nakajima, C. 1936. (cult.) . . . . $2n = 24$
Neves Barros, J. de. 1952. (Portugal) . . . $2n = 22 + 2$

MELIACEAE

Melia azedarach L.
coll. no.: 169 . . . . $2n = 28$
origin: roadside in Tortosa (prov. of Tarragona)
references:
Bowden, W. M. 1945. (cult.) . . . . $2n = 28$

PAPILIONACEAE

Lathyrus articulatus L.
coll. no.: 122 . . . . $2n = 14$
origin: coastal road near Marbella (prov. of Malaga)
references:
Senn, H. A. 1938. (cult.) . . . . $2n = 14$

Lotus ornithopodioides L.
coll. no.: 120 . . . . $2n = 14$
origin: roadside between Motril and Malaga, near Almuñécar, (prov. of Granada)
references:
Senn, H. A. 1938. (cult.) . . . . $n = 7$
Tschechow, W. V. *et al.* 1932 (cult.) . . . . $2n = 14$
Larsen, K. 1955a. (Tunesia, Italy) . . . . . $2n = 14$

Medicago orbicularis (L.) All.
coll. no.: 15 . . . . $2n = 16$
origin: El puente del diable, N. of Tarragona (prov. of Tarragona)
references:
Ghimpu, V. 1928, 1930. (cult.) . . . . $2n = 16$
Fryer, J. R. 1930. (cult.) . . . . $2n = 16$
Larsen, K. 1955. (Italy) . . . . $2n = 16$
Heyn, Ch. 1956. (Israel) . . . . $2n = 16$

Vicia sativa L.
coll. no.: 16 . . . . $2n = 12$
origin: El puente del diable, N. of Tarragona (prov. of Tarragona)
references:
Sweschnikowa, I. 1927. (cult.) . . . . $2n = 12$
Bleier, H. 1929. (cult.) . . . . $n = 6$
Sweschnikowa, I. *et al.* 1936. (cult.) . . . . $2n = 12$
Senn, H. A. 1938. (cult.) . . . . $2n = 12$
Moriya, A. and A. Kondo. 1950. (Japan) . . 6, 7
Larsen, K. 1956. (Italy) . . . . $2n = 12$
Yamamoto, K. 1961. (Morocco) . . . . $2n = (10)\ 12$

PRIMULACEAE

Coris monspeliensis L.
coll. no.: 44 . . . . $2n = 56$
origin: dunes near Albufera, lagoon S. of Valencia (prov. of Valencia)

RANUNCULACEAE

Ranunculus acetosellifolius Boiss.
coll. no.: 98 . . . . $2n = 16$
origin: near University inn in Sierra Nevada, ± 2500 m (prov. of Granada)

ACKNOWLEDGMENT

These investigations have been carried out in the Botanical Museum and Herbarium of the State University of Utrecht, the Netherlands (Director Prof. Dr. J. Lanjouw).

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BRIEF REPORT

Th. W. J. Gadella: Some cytological observations in the Loganiaceae III

Previously, the chromosome numbers of some species of *Loganiaceae* were dealt with (Gadella, 1961, 1962, 1963). The chromosome numbers of 7 species are reported in this paper, of which 4 species, all belonging to the genus *Strychnos*, had not been investigated cytologically before. The materials, kindly supplied to me by Dr. A. J. M. Leeuwenberg and by Ir. F. Breteler, were collected in the form of seed-samples in the Ivory Coast and in Cameroun. The plants of 2 species originate from botanical gardens. Living material of all species (except for *Strychnos ternata* Gilg. ex Lwb.) is grown in the botanical garden of Wageningen (WAG). The determination of the chromosome numbers was based on the study of roottip-mitoses. Roottips of the plants were fixed in Karpechenko, embedded in paraffin, sectioned at 15 micron and stained according to Heidenhain's haematoxylin method. The results may be summarized as follows:

1. *Nuxia floribunda* Benth.: $2n = 38$
   Origin of the material: S. Africa, obtained from the University of Stellenbosch. Seeds probably collected in the wild.
   Herbarium material of the mother-plant: J. J. Bos, no. 310 (WAG).
   Herbarium material of seedling: A. J. M. Leeuwenberg no. 3665 (WAG).
   References: Gadella (1963): $2n = 38$.

2. *Strychnos dinklagei* Gilg.: $2n = 44$
   Origin of the material: Ivory Coast, Forêt d'Abouabou, between Abidjan and Grand Bassam.
   Herbarium material of the mother-plant: R. A. A. Oldeman no. 845 (WAG).
   Herbarium material of the seedling: A. J. M. Leeuwenberg no. 3561 (WAG).
   References: Gadella (1963): $2n = 44$.

3. *Strychnos innocua* Del. subsp. *innocua*: $2n = 44$
   Origin of the material: Ivory Coast, 16 km S. of Ferkéssédougou.
   Herbarium material of the mother-plant: A. J. M. Leeuwenberg no. 4435 (ABI, WAG).

4. *Strychnos millepunctata* Leeuwenberg: $2n = 44$ 1)
   Origin of the material: Ivory Coast, Forêt d'Abouabou, between Abidjan and Grand Bassam.
   Herbarium material of the mother-plant: J. J. F. E. de Wilde & A. J. M. Leeuwenberg no. 3447 (ABI, WAG).

5. *Strychnos samba* Duvign.: $2n = 44$
   Origin of the material: Cameroun, 4 km S. of Nguélémendouka.
   Herbarium material of the mother-plant: F. J. Breteler no. 2051 (WAG).

6. *Strychnos spinosa* Lam.: $2n = 44$
   Origin of the material: obtained from the botanical garden of Groningen, the Netherlands, origin unknown.

Herbarium material of cutting: A. J. M. Leeuwenberg no. 3564 (WAG).
References: Mangenot and Mangenot (1958): $2n = 44$.
Miège (1960): $2n = 44$.
Gadella (1962): $2n = 44$.

7. *Strychnos ternata* Gilg. ex Leeuwenberg: $2n = 44$ [1]
Origin of the material: Cameroun, 27 km from Bertoua on road to Bétaré Oya.
Herbarium material of the mother-plant: F. J. Breteler no. 2196 (WAG).
Herbarium material of the seedling: F. J. Breteler no. 2994 (WAG).

Twenty-one species of the genus *Strychnos* have been studied up to the present. The following chromosome numbers have been counted: $2n - 24$ (3 species, counted by Mohrbutter, 1936); $2n = 44$ (16 species); $2n = 88$ (2 species). From these data the conclusion may be drawn that the more common basic number of the genus *Strychnos* is $X = 11$ or $X = 22$.

ACKNOWLEDGEMENT

These investigations have been carried out in the Botanical Museum and Herbarium of the State University of Utrecht, the Netherlands. Director: Prof. Dr. J. Lanjouw.

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[1] These species were recently described by A. J. M. Leeuwenberg (Acta Botanica Neerlandica **14**: 218–229. 1965).

BOOK REVIEWS

J. B. Thomas, Primary Photoprocesses in Biology. North-Holland Publishing Company, Amsterdam, 1965; 333 pp., Dutch Guilders 36.—.

In the scientific literature on photobiology one often can read statements which have great shortcomings from the point of view of physics.

It is not always realized that when a biologist is experimenting in photobiology he should know not too little about the fundamentals of the physics of light. Usually literature about this subject is meant for physicists and therefore not easily understood by biologists. The book of dr. Thomas however is a book for biologists written by a biologist.

In the first chapters dr. Thomas gives us an insight in the physics and chemistry of the photobiological processes which occur in nature. He does this in such a way that it is quite understandable for a biologist.

Then he turns to the biological phenomena themselves. First comes an up to date picture of the fundamentals of photosynthesis according to modern views. This is important because most of the handbooks for students in biology are not quite modern when discussing photosynthesis.

Then comes vision. Different structures of eyes are given, the visual pigments are discussed. Afterwards one finds chapters on phototaxis, photokinesis, photodinesis, phototropism and photomorphogenesis. Many of these phenomena have different photoreceptor pigments and therefore are of great interest to the student of photobiology.

A last chapter is dedicated not to the effect of illumination but to emission of light by organisms: bioluminescence. This subject stands more or less apart from the other phenomena but on the other hand it should be discussed in a book on "Photoprocesses in Biology".

This book is not only most valuable but in fact quite necessary for biologists and students in biology as soon as they are confronted with problems of photobiology. For a plantphysiologist it is practically impossible to evade photoprocesses; for a zoöphysiologist light plays a less dominating role although in the life of animals too photoreactions often are very important.

Therefore dr. Thomas' book deserves a welcome reception from all biologists who are interested in physiology.

R. VAN DER VEEN

Konrad Mengel (Giessen), Ernährung und Stoffwechsel der Pflanze. VEB Gustav Fischer Verlag, Jena, 1965, revised edition; 34.— DM.

Although a review of the first edition has already been given in volume 12, pag. 354 of the journal in 1963 by van Die, it does seem worthwhile to once more direct attention to this excellent book. The nutrition of the plant is treated in a wide sense. Besides the relevant metabolic processes, the fertilisation and the nutrient medium, the soil, are thoroughly treated.

The book will thus be primarily of value for agronomy students. As the author, however, has managed to treat this important subject in such a wise as to give a concise and integrated review in an excellently readable manner, it should also be able to give others, experts in this field included, worthwhile information. This characteristic of the book is due to a lucid style, an orderly division of subject matter and a certain contemplativeness, which, however, never leads to a verbosity sometimes inherent to German books. The problems are always clearly and concisely defined and elucidated by means of a single example, usually derived from recent literature. As a result the book is up to date. A small drawback of this procedure is, that older important literature has to be somewhat neglected.

It is evident that the author has taken into account criticisms on the first edition; some chapters have been rewritten or extended. Nevertheless the text has been kept down to 331 pages, despite an extension of 50 pages.

In a first part the general significance and the functions of the nutrients are dealt with. Besides chapters on the soil, the uptake of nutrients, the physiological and biochemical principles of the separate metabolic processes, chapters are included on the relationships between nutrition and yield and quality of the crop. In this first part the clear exposition of the yield laws, in which the above mentioned relationships are formulated, and the significance of the interrelationships of the different factors merits special attention.

In a second part the nutrient elements are treated separately. For each element occurrence in the soil, absorption and function in the nutrition of crop plants is elucidated.

This classification of the matter can be considered justified, although a different one is conceivable. The same holds for the choice of examples. The opinion of the reviewer is that the author has made a good selection.

The treatment of the problems related to soil science is good and also those on fertilization. The Dutch reader may regret the absence of information, which is of special importance to him, e.g. the fertilization of permanent grassland and a more detailed discussion on the applicability of soil analysis for determining fertilization requirements. As a result of the concise treatment some omissions are inescapable. Also the symptoms of excess zinc could have been mentioned in the appropiate part. A few shortcomings and faults, which will be noticed in the text, however, do not invalidate the favourable impression. It might be mentionde that the photographs of deficiency symptoms could be improved upon.

In conclusion a book, which reads very well and may be the best in its realm. For a more detailed review on the physiological chapters reference may be made to the previous review by van Die.

Acknowledgements are due to my colleagues dr. W. van Driel, dr. ir. K. W. Smilde and dr. L. K. Wiersum for reading chapters related to their field of specialisation. The writer of this review has been happy to utilize their opinion.

F. VAN DER PAUW

ELSEVIER'S WOOD DICTIONARY in seven languages. Volume 1, Commercial and botanical nomenclature of world-timbers; sources of supply, compiled and arranged by W. Boerhave Beekman. Elsevier Publishing Company, Amsterdam, London, New York, 1964. xxii + 479 pp., 4 figs. D. fl 55.—; £ 5.10.0.

During the congress of wood-experts held at Stuttgart in 1953, it became evident that a multilingual dictionary of world-timbers was urgently needed in order to conquer the great difficulties caused by the use of many confusing or even misleading commercial names for several kinds of timber. Dr. Boerhave Beekman, Director of the Netherlands Wood Academy, Amsterdam, and well-known wood-expert, was asked to work out plans for such a book.

Now the first result of Dr. Boerhave Beekman's immense work lies before us. It is the first volume of a Wood Dictionary, volumes 2 and 3 of which will contain Production, transport, trade, and Research, manufacture, and utilization respectively.

This first volume mainly consists of two large tables. The first and basic one contains in alphabetical order no less than 3778 English and American names of kinds of wood with their French, Spanish, Italian, Swedish, Dutch, and German equivalents, and their sources of supply. The second table gives the scientific names of exactly 2500 botanical species together with a large number of synonyms, also arranged alphabetically, with cross-references to the first table. Alphabetical lists of the names in various other languages used in the dictionary are found at the end of the book. It is to be regretted that in the second table the author did not add the names of the families to the generic names. This would have been a useful addition especially for those users of the book who are not fully acquainted with the numerous tree genera mentioned.

This first volume, and I suppose also the two volumes still to appear, will be of great value to everyone concerned with forestry, timber, wood products, or economic botany in general. Let us hope that it will become the basis for a greater uniformity especially in commercial nomenclature of timbers.

S. J. van Ooststroom

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PROBLEMS AND USE OF STRUCTURE IN THE CLASSIFICATION OF VEGETATION

THE DIAGNOSTIC EVALUATION OF STRUCTURE IN THE BRAUN-BLANQUET SYSTEM

V. WESTHOFF

(*State Institute of Nature Conservation Research* (*RIVON*), *Zeist, the Netherlands*) (*RIVON-communication nr. 228*)

(*received November 11th, 1965*)

1. Introduction

It is a well-known fact that vegetation can be classified on the basis of quite different criteria; e.g. by physiognomy, structure, dynamic processes, floristical composition, and even – a scientifically less satisfying way – by habitat. It is not the aim of this study to give a critical review of these starting-points. The author's purpose is to consider the Braun-Blanquet system of vegetation classification, which is a system claiming to be based on floristical composition, and to analyse how far, in reality, structural criteria are involved in it. This article does not consider whether Braun-Blanquet syntaxonomy is the only valuable or even the best one. In fact it is, however, the most widely used and uniform system of vegetation classification, enabling us to compare plant communities over an area as large as (e.g.) Europe, and, therefore, also presenting a basis for such items as geographical comparison of habitats, vegetation mapping of large areas, or the analysis of geographical differences in the autecological behaviour of taxa.

It may thus be useful to see whether the higher units of this inductive system correspond to the units of the more or less deductive formation systems of the world, based on physiognomy and structure.

The International Botanical Congress of Brussels (1910) defined the concept of association as a unit of vegetation which is floristically, ecologically and physiognomically homogeneous. From this starting point Braun-Blanquet (1913, 1928, 1932, 1951, 1964 etc.) has especially emphasised the diagnostic value of the floristic composition in its aspect of faithfulness, i.e. the rate, in which taxa appear to be bound to one or several communities (see also Becking, 1957; Poore, 1955; Cain and Castro, 1959; Westhoff *et al.*, 1951, 1965). At first sight such a system may appear an artificial one, since it deals with one feature of vegetation only. Against this viewpoint it may be argued, that the concept of faithfulness is a synthetic one, based on a number of analytical and synthetical characters of the vegetation such as abundance, dominance, sociability, vitality, fertility, stratification, periodicity and presence. As a matter of fact, this floristic classification is based on quite a complex of features and not on a single one. Another objection, however, is more essential. The fundamental hypothesis of Braun-Blanquet, formulated as early as 1913, states that the floristic composition represents all the other characters of the vegetation, since each taxon presents its own ecological amplitude, its specific genetic and historical background and its characteristic dynamic behaviour. Therefore, the floristic relations would be correlated with ecological, chorological and dynamical relations. For this reason the Braun-Blanquet system may be stated to be more a natural than an artificial one.

Since 1913, a number of investigations have proved this hypothesis to be valuable. Nevertheless the claimed correspondance has its exceptions, as is the case with most laws in biology. There are cases in which the floristic composition varies more or less independently of the other characters of vegetation. Such exceptions offer syntaxonomical problems. We will restrict ourselves here to structural problems: (1) the problem arising when two or more plant communities or higher vegetation units appear to be floristically closely related, but quite different in structure; (2) a problem of relative homogeneity, viz. the case of vegetations with a complex mosaic pattern of structure, posing the question as to the level at which this complexity has to be taken into account in a classification system based on floristic composition.

Before entering into these topics the possibility of coordination between any formation system and the Braun-Blanquet system has to be considered (see also Lam, 1948; Cain and Castro, 1959; Doing, 1962; Van Donselaar, 1963; Westhoff *et al.*, 1965). The often abused term "formation" is used here in its original sense as given by Grisebach (1872) and applied a.o. by Beard (1944) and Cain and Castro (1959).

The Braun-Blanquet method is an inductive "micro-method", built into a hierarchical system. It operates with units which from low to high contain more lower units and are every time characterised by species with larger ecological amplitudes; at the same time, these larger units are related to more comprehensive ecosystems, greater structural variance and larger distribution areas. Until some years ago classes were the highest unit; recently Braun-Blanquet (1964) has added class groups. A class group has few or no species in common, but it is characterised by taxa of higher rank consisting of vicarious species: e.g. the class group of deciduous forests on rich soils in the northern temperate zone. The class groups represent the ultimate classificatory possibility in a system having a floristic basis. It would be desirable now, to circumscribe the classes or class groups in such a way, that they fit in well with the units of a formation system. Even if purely floristically diagnostic criteria are used, this wish can be fulfilled, since a method based on floristic composition may lead to more than one possible system. An example is the mediterranean class of *Cisto-Lavanduletea* with the order *Lavanduletalia stoechidis* and *Helianthemetalia guttati*. The first order consists of low shrubs in an open habitat, the second of open grassland and herbaceous communities. The latter however has a number of faithful species in common with the order *Festuco-Sedetalia*, dry grasslands of the extra-mediterranean region of Western and Central Europe, such as *Helianthemum guttatum*, *Jasione montana*, *Aira caryophyllea*, *Silene gallica*, *Trifolium striatum*, *T. subterraneum*, *Hypochoeris glabra*, *Vulpia bromoides*, *Filago gallica*, *F. minima*, *Poa bulbosa* and *Vicia lathyroides*. It would, therefore, be quite possible to split the *Helianthemetalia* from the *Lavanduletalia* and to join the former with the *Festuco-Sedetalia* in one class. BRAUN-BLANQUET too, has recognised the importance of this structural difference: in 1931 he joined the alliance of *Helianthemion guttati* to the *Lavanduletalia*, but in 1940 the former unit was given the rank of an order (BRAUN-BLANQUET, MOLINIER and WAGNER, 1940).

Joining the *Helianthemetalia* and *Festuco-Sedetalia* would result in a classification more homogeneous and logical from a structural viewpoint. The objection may be made, that a combination of a mediterranean and a non-mediterranean order to one class is undesirable, but such a chorological consideration has just as little to do with classifying on a floristic basis as a structural argument has. In this paper the author does not intend, however, to join the orders *Helianthemetalia* and *Festuco-Sedetalia*; more elaborate argumentation would be necessary. The case was only meant to present an example of how a certain group of communities can be classified in two structurally different ways, both on the basis of a floristic method.

Quite another approach in coordinating structural and floristical vegetation classification has been tried by VAN DER MAAREL and WESTHOFF (1964), who established a system of local dune plant communities primarily on structural, secondarily on floristical criteria.

2. CONCEPTS OF STRUCTURE IN SPACE AND TIME

One of the clearest expositions on the criteria used in classifying vegetation has been given by FOSBERG (1958), who distinguished between physiognomy, structure and function. Physiognomy, the aspect of vegetation, is a much less exact or objective feature than structure and function and leads to categories such as wood, shrub, swamp and desert. The systems of SCHIMPER (1898) and RÜBEL (1930) and also the "formation types" in the sense of DANSEREAU (1958) are physiognomical. On the contrary, according to FOSBERG (l.c.) structure is the order of vegetational components in space. The concept of structure has been defined in various ways. Many authors limit it to stratification and horizontal pattern; others, e.g. DANSEREAU (1958) include periodicity, life forms, growth forms, leaf characters and seed dispersal. FOSBERG (l.c.) proposes to limit the concept of structure to the spatial distribution of vegetation biomass and to exclude all adaptative phenomena which are functional – or presumed to be functional –; the latter should be brought together under the concept of function. The present author prefers a middle course and assigns to structure also: (1) structure in time (see below);

(2) spatial pattern based on the distinction of life forms which are easily distinguished morphologically, e.g. those defined by RAUNKIAER or by IVERSEN (1936). A similar concept of structure has – in an implicit way – also been used by CAIN and CASTRO (1959). The practical use of such a concept of structure has been proved by the symbol diagrams of DANSEREAU (1958), which have been applied by DANSEREAU and ARROS (1959) to their structural diagrams of 83 European associations.

It has to be stressed now that structure should not only be considered and studied in its static and spatial aspect. MARGALEF (1958, 1961) distinguished, within the concept of structure two aspects viz. the static or compositorian aspect, which I have discussed so far, and the dynamic or energetic. The latter deals with the energy flow in ecosystems. The present author will not agree with this viewpoint; in his opinion, this dynamic structural concept of MARGALEF has hardly anything to do with structure. Structure is a matter of form and not of energy. I shall elucidate the connection between the static and the dynamic aspect of structure from another viewpoint, that of systems theory.

As a result of succession analyses carried out for about twenty years on some hundreds of permanent quadrats in the various vegetation types of the Netherlands, VAN LEEUWEN (1960, 1962, 1964, 1965, 1966a, 1966b) has worked out the mutual relations between spatial structure and dynamic behaviour, i.e. between pattern and process, and has proposed an ecological systems theory, based upon the general systems theory of ROSS ASHBY (1958). This theory has proved to be useful in the first place in research on ecological gradients and borderline areas (see also TÜXEN and WESTHOFF, 1963; WESTHOFF, VAN LEEUWEN and ADRIANI, 1962; VAN DER MAAREL, WESTHOFF and VAN LEEUWEN, 1964; WESTHOFF, 1965; WESTHOFF and VAN LEEUWEN, 1965). In this theory, isolation and communication have been opposed to each other. Isolation appears to induce differentiation, whereas communication leads to egalisation. Differentiation in space is furthered by continuity in time; the reverse is also true: continuity in time effects a more differentiated spatial pattern. On the other hand, homogeneity in the spatial pattern and poverty in species are linked with disturbances, discontinuities in time. On the basis of these experiences two borderline ecosystem types have been discerned: the unstable or convergent limit and the stable or divergent limit.

A convergent limit is characterised by concentration effects, thus by easily recognisable, sharp contours, coarse-grained patterns and instability. A divergent limit is characterised by effects of spreading, thus only with difficulty recognisable, vague contours, fine-grained patterns and stability. Convergent limits are to be found in unstable transitional zones between ecologically extreme situations. More or less synonymous concepts are: ecotone, stress zone, tension belt, disturbance zone, noise environment, shuttle environment. The horizontal convergence is often combined with a vertical one (soil hardening). Divergent limits are to be found in stable, transitional zones, with complex gradient structures. More or less synonymous is the concept of ecocline (see VAN DER MAAREL and WESTHOFF, 1964).

I shall return to these two types of border situations in discussing the increasing importance of structure in the Braun-Blanquet classification system.

3. RELATIVE INDEPENDENCE OF LAYERS AS A PROBLEM IN CLASSIFICATION

Different stands of vegetation may have one or more layers in common, whereas the remaining layers are different. HULT (1881) was the first botanist to make use of this phenomenon in classifying communities. He described sixteen "twin formations", e.g. the *Pineta polymorpha*: these formations had *Pinus sylvestris* dominant in the tree layer (combining stand), and whereas in one formation *Vaccinium myrtillus* and *Hylocomium splendens* formed the ground layer, in the other formation, their place was taken by *Calluna vulgaris* and *Cladina* spp. (alternating stands). The older school of Russian plant sociologists further developed the method (KELLER, 1927; SUKACHEV, 1928; KATZ, 1929; ALECHIN, 1932). KATZ produced the concept of homologous series of twin communities, in which both structure and ecology are taken into account. In one of the first analyses of vegetation on the Dutch dunes this method was similarly applied (BIJHOUWER, 1926). In a somewhat different way the idea has been developed by LIPPMAA *et al.*(1934) and by DU RIETZ (1921, 1932, 1936) and his students; the latter named the stratal units, considered by them as independent ones, Sozietäten, later on Konsozionen, whereas the former named them "unions", a term approved by the International Botanical Congress of Amsterdam (1936). These concepts present special cases of the synusia concept of GAMS (1918). It has been shown (e.g. by CAIN and CASTRO, 1959) that such a classifying method is functional for northern Eurasia, viz. in boreal areas with a relatively simple vegetation structure, where many species are able to dominate alternatively; in warmer areas with more complicated structure and decreasing dominants it is not practical however. According to CAIN and CASTRO (l.c.) a classification system on a synusial basis can be useful only in regions whose floras are poor in species and where environmental conditions are critically limiting; they refer to ROACH (1952), who studied a mountainous area of vulcanic origin. Certainly the difference between extreme and non-extreme habitats is of great importance; it will be shown below that such twin formations are not bound to boreal and alpine circumstances, but are to be found even in the tropics. My viewpoint, however, is not so much whether it is possible to classify vegetation on the basis of synusiae, but what the consequences of relative layer independence are for the Braun-Blanquet system.

A simple example showing that in some cases structure has always been the main diagnostic criterion in this otherwise floristical system, is presented by deciduous swamp woods compared with the stands of tall herbs derived from them after cutting ("Hochstaudenfluren"). The floristical resemblance between certain swamp woods and certain herb swamps is so great, that they could very well be joined into one alliance, a consequence, however, which no author as yet has drawn: these communities are assigned to different classes. It is true that the floristical difference between a well developed canopy of *Alnetum glutinosae* and a *Valeriano-Filipenduletum* or *Filipendulo-Geranietum* is still considerable. The difference decreases when we deal with an open *Alnetum*-coppice; but all syntaxonomists of the Braun-Blanquet system agree that only optimally developed stands may be used for classifying purposes. However, there are also, and especially on mineralised peat soils, alder marshwoods belonging to the alliance *Alno-Padion* – e.g. the *Macrophorbio-Alnetum* –, which only show small floristical differences with a comparable *Valeriano-Filipenduletum* in the same area, and it is only on structural grounds that it can be justified in assigning these associations to different classes, viz. *Querco-Fagetea* and *Molinio-Juncetea.*

Just the opposite solution however has been given in the case of the *Rhodoro-Vaccinion*, as it has been dealt with by BRAUN-BLANQUET, SISSINGH and VLIEGER (1939). The climatic climax of the upper subalpine zone in large parts of the Alps is the *Rhodoro-Vaccinietum.* This association has been divided into four subassociations: *mugetosum*, with *Pinus mugo*; *cembretosum*, with *Pinus cembra*; *calamagrostidetosum* and *extrasilvaticum*, i.e. without a tree layer. In this case, therefore, communities of different formations have been joined into one association indeed. It is true that the *Rhodoro-Vaccinietum pinetosum* and *cembretosum*, open mosaic communities near the timber line, can hardly be considered to be woodland; especially as the succession tendancy of the subassociation *cembretosum* is so easily disturbed by man, that a *Pinus cembra* canopy is hardly to be found anywhere. If such a well-developed canopy were described, it might be considered an association of its own, but still as a part of the alliance *Rhodoro-Vaccinion.*

Similar situations are found in subartic and circumboreal Fennoscandia, Russia and Siberia. In wind-exposed habitats near the timber line occur the communities of the *Loiseleurio-Vaccinion*, consisting mainly of "Spaliersträucher" such as *Loiseleuria procumbens* and *Diapensia lapponica* and of lichens. In the next lower zone birch woods and birch-pine woods occur, e.g. *Cladonio-Betuletum tortuosi* and *Hylocomio-Betuletum tortuosi*, the "twin formations" described by HULT and KATZ. The latter have been joined to the alliance *Phyllodoco-Vaccinion*, which together with the *Loiseleurio-Vaccinion* have been assigned to the *Vaccinio-Piceetalia*, although the structures of these alliances differ considerably. However, any botanist who knows these vegetations personally will agree that any other syntaxonomical approach to these little floristical differences between woodland and nanophanerophyte carpets would be difficult.

A comparable situation in Ireland has been described by BRAUN-

Blanquet and Tüxen (1952). The eu-atlantic Irish association of the deciduous woodland alliance *Quercion roboris-petraeae* has been named by them *Blechno-Quercetum*. On very wet and nubulous slopes of maritime mountains (McGillycuddy reeks, Co. Kerry) a community of *Luzula maxima* occurs, which should be considered a degradation stage of woodland. Braun-Blanquet and Tüxen described this community as *Blechno-Quercetum extrasilvaticum*, although in these surroundings no single tree can be found. This solution seems an odd one, but after having visited the classical spot the present author agrees that within the Braun-Blanquet system no other description would be logical or practical.

A similar problem is offered by the wooded raised bogs in the baltic area. Their nanophanerophyte communities with more or less scattered trees in them have been described as a class *Vaccinetea uliginosi* with the order *Vaccinietalia uliginosi* and the alliances *Betulion pubescentis*, *Piceo-Pinion uncinatae* and *Pino-Ledion palustris*. Lohmeyer *et al.* (1962) have rejected these higher units and joined them to woodland alliances, but this solution is clearly at variance with the syntaxonomic trend of today. Situations of the above kind are not only found in the cool North or the wet atlantic West, but equally in the mediterranean region. A good example is the garigue of southern France, the *Rosmarino-Ericion*, and especially its association *Rosmarino-Lithospermetum*. The structure of this association has been studied in detail by Barkman (1958b). It presents a number of subassociations, of which four may be mentioned, constituting a degradation cline from woodland to dwarf shrub formation: *R.-L. pinetosum halepensis*, a "savanna" of Aleppo pine; *R.-L. ericetosum multiflorae*, a homogeneous closed dwarf shrub community; *R.-L. helianthemetosum*, a mosaic complex of dwarf shrub stands and open herb vegetations; and finally *R.-L. schoenetosum*, where dwarf shrubs are minor components. In this case also communities with considerably different structures have been joined into one association. Dansereau and Arros (1959), who consider structure as a major diagnostic feature, are strongly opposed to this example of classification, their attack being directed against Guinochet (1955).

Even in the tropics situations are found where the vertical bond between the vegetation layers is only loose and the stands consist of more or less independent synusiae. Meyer Drees (1951) described such a case from the savannas of the Indonesian island of Timor. In these savannas scattered tree groups of various densities occur, on a certain substrate *Eucalyptus alba*, on another *Acacia leucophloea*, etc. In the Eucalyptus savanna in particular the herb layer under the trees appeared nearly the same as in the open stands. In spite of the great difference in structure it was necessary, therefore, to join the grassland community and savanna into one association. Meyer Drees (l.c.) however did not like this solution and would prefer to distinguish locally dominante communities on the basis of constancy (Scandinavian method). Similar patterns were recorded from Timor mangrove.

Van Donselaar (1963) investigated the savanna vegetation of Surinam on soils with alternating water levels. He found that the Braun-Blanquet method was appropriate to these vegetation types and he was the first botanist in the northern part of South America to develop a system of associations, alliances, order and classes. He too met the problem that, in some cases, the undergrowth of savanna tree stands differed so little from the open herb vegetation without a tree layer, that both had to be reckoned as the same association. Contrary to Meyer Drees (l.c.) and Dansereau and Arros (l.c.) however, Van Donselaar is quite convinced that the floristical principle must preponderate and that, in this case, it would be unlogical to try to place tree stand and grassland in different classes. He prefers an association system quite separate from a formation system of the same vegetations and independent of each other.

The examples mentioned show that the problem of twin formations with rather independent layer synusiae, in other words the phenomenon of stands differing little in floristical but strongly in structural respects, is bound to extreme habitat conditions. Certain abiotic or even biotic environmental factors preponderate here (master factors) and outdo the ecological influence of a tree layer on its undergrowth. In subarctic, boreal and subalpine areas cold winters, snow cover and wind are all-important; in oceanic climate the high air humidity; on wooded raised bogs the deficiency of nutrients and oxygen in the soil; in the savannas of Timor and Surinam the extremely alternating water levels, in the mediterranean garigue the frequent burning by man. In these cases structure has a minor ecological importance indeed, so that it should not be overestimated as a diagnostic criterion. So I agree with Van Donselaar (l.c.) as to his syntaxonomic solution for the present problem, which does not mean that I agree with his principal objections against the coordinating of floristical and structural systems.

4. The increasing weight of structure in the Braun-Blanquet method

Hitherto I nearly took for granted, that all layers of a stratified community should be studied in their totality as a single phytocenosis; the unistratal concept of Lippmaa and Du Rietz has only been mentioned (see also Cain and Castro, 1959). Without entering deeply into this matter, it should be remarked that this assumption does not hold in all cases. Epiphyte communities (see Barkman, 1958b) are generally held to be an exception, because their habitat is rather independent of the soil. However, it is not always easy or even possible to separate the epiphyte community from the phanerogam stand; moreover, the limit between epiphytic communities and cryptogamic communities on the soil surface is often difficult to draw. This problem of microcenoses has been thoroughly dealt with by Barkman (1965). Apart from such problems, Zürich-Montpellier workers generally agree that synusiae rooting together in the same substrate have to be considered one total plant community. There are, however, exceptions also to this rule. TÜXEN (1950) described the "Schleiergesellschaften" (liane blanket communities) of river banks and similar convergent ecotones as an alliance *Calystegion sepii*. We have here to do with an outpost of a type of vegetation structure which is much better developed in the tropics. In fact, the associations of the *Calystegion sepii* are synusial units, although they are not claimed to be so. This solution should not be recommended, because of analytical difficulties. It is hardly possible in making sample plot analyses (relevés) to separate the blanket lianes from the other species which are also rooting in the same substrate. The result would be a subjective choice as to which species should be included in the list and which not.

Yet a special case is presented by the water vegetations. Previously the different strata of water communities, viz. the bottom or isoetid layer, the suspended or elodeid layer, the swimming-and-rooting or nymphaeid layer and the only just swimming or lemnid layer, have generally been joined into one association, although the analogy with terrestrial vegetations is not very obvious. In fact, the hydrophyte strata appear to be much less interdependent than the terrestrial ones; for the greater part they do not live in the same micro-habitat. This fact has been taken into account firstly in subdividing the lemnid strata into separate units: the alliance *Lemnion*, the order *Lemnetalia* and the class *Lemnetea* (MIYAWAKI and TÜXEN, 1960). DEN HARTOG and SEGAL (1964) and SEGAL (1965) have followed up the consequences of this development. They composed a system based not so much on strata as on life form synusiae, thus splitting up the former class *Potametea* into the classes *Potametea* s.s., *Ceratophylletea*, *Utricularietea*, *Stratiotetea* and *Lemnetea*. An important argument in its favour is the pioneer character of most hydrophyte communities, which brings about rapidly changing structures with often monospecific vegetation masses; a problem which will be dealt with below.

Not only in the case of the *Potametea*, but also in that of helophyte communities of the orders *Phragmitetalia* and *Montio-Cardaminetalia* there are many examples of coarse mosaic patterns, in which large monospecific clusters of individuals (often clones) are alternating. Often such a pattern is bound to primary abiotic habitat differences: for instance in *Scirpo-Phragmitetum*, *Typha angustifolia* dominates on soft mud, *Scirpus lacustris* in the deepest zone most exposed to wind and waves, etc. A general analytic procedure in the Braun-Blanquet method is that such a pattern, brought about by primarily abiotic factors, leads to the distinction of several associations within this pattern. However, the large association *Scirpo-Phragmitetum*, first described by W. Koch in 1926, as yet has not been split up, but undoubtedly such a splitting will prove to be desirable in near future; a unit like the *Scirpo-Phragmitetum* is becoming an anachronism.

There are, indeed, many examples showing that the Braun-Blanquet method in recent years, mostly in Western and Central Europe, is more and more insisting on structure as a diagnostic criterion. This development is obvious in pioneer communities as well as in terminal (climax) ones. In 1936, the stands of *Salicornia europaea* and *Spartina stricta* on northwestern-atlantic marine mud flats were still considered to compose one association (BRAUN-BLANQUET and DE LEEUW, 1936); more recently they have even been made into two classes, *Thero-Salicornietea* and *Spartinetea* (TÜXEN and OBERDORFER, 1958; LOHMEYER *et al.*, 1962; BEEFTINK, 1962, 1965). One reason for this change is the great difference in life forms: the stands mentioned present two synusiae, the former a therophyte, the latter a geophyte one. However, a more important factor is that here we have to do with pure stands very poor in species. A careful analysis always points out that a well-developed *Salicornia* stand and an equally well developed *Spartina* stand have no single species in common, so that they do not have any floristical relation (as far phanerogams are concerned). This situation, common in pioneer vegetation, will urge us more and more to what PIGNATTI (1964) called "the inflation of the higher vegetation units". It is essential to realise that in such cases we have to do with patterns of unstable habitat, i.e. communities of convergent ecotones or convergent areas which in the course of time are exposed to irregular major ecosystem fluctuations and changes. Other examples are the *Ruppietea* of the poikilohalinic (brackish) water, the *Cakiletea* of the tidal marks on the sea shore, and the *Plantaginetea maioris* of the border areas between the extremes of wet and dry, salt and fresh, trodden and untrodden, and soil rich and poor in nutrients. In all such cases the analysis of vegetation is relatively simple, but the development of a hierarchic system is difficult; as an overstatement it might be said that every two associations from this type of environment represent two classes. (See also VAN DER MAAREL, WESTHOFF and VAN LEEUWEN, 1964).

In contrast to this category are the stable, divergent gradient communities, rich in species, with fine-coarsed pattern and vague contours, living in a stable environment where fluctuations (if any) are rhythmic and regular. In such cases vegetation analysis is more difficult: the problem is where the limits between the relevés have to be drawn and which level of homogeneity should be taken as a basis for classification. As a result of this problem, the syntaxonomy of the woodland margin communities in particular, the "mantles" (shrub) and "skirts" (borderlines of tall herbs), was somewhat neglected up to about 1950. In later years however this situation changed, at least in Western and Central Europe, on account of a gradual refining of analytical methods and of special attention to the close and intricate contact of two or more adjacent communities gradually merging into each other within a complicated divergent border pattern.

TÜXEN (1952) made an important development on the Braun-Blanquet system in a classification which is to a larger extend based on structure. He joined the mantle communities of woodland margins with comparable communities of shrubs and hedges into one newly described order, named *Prunetalia spinosae*. This order was assigned to the class *Querco-Fagetea*, described as early as 1937 by BRAUN-BLANQUET and VLIEGER. The admission of the order *Prunetalia* is contrary to the generally accepted subdivision of the *Querco-Fagetea*. This consequence could have been avoided if all newly described shrub and mantle associations had been left near their edaphically and chorologically corresponding woodland associations, so that each shrub association would be placed in the same alliance at least as its comparable woodland companion. This solution, which has already been tried by JAKUCS (1961) is possible, because by far the most shrub associations have a part of their faithful and differential species in common with the corresponding (often adjacent) forest associations. TÜXEN, however, (l.c.) choose another way, with the result that, in this case, the structural criteria have superseded the floristical ones. It must be added that this renovation has been agreed with all over Europe and that it has induced much new valuable research. The next consequence was to raise the *Prunetalia* to the rank of a class. This has been effected independently by three authors: the Spanish botanists RIVAS GODAY and BORJA CARBONELL (1961) described the class *Rhamno-Prunetea* (referred to in TÜXEN, 1962); TÜXEN (1962) himself proposed the name *Crataego-Prunetea*; DOING (1962) the name *Sambucetea*. For the sake of priority *Rhamno-Prunetea* is the valid name. The *Prunetalia* are structurally similar and phytogeographically vicarious to that thorn shrub formation of the mediterranean mountains and southern continental areas, which was first described by ADAMOVIČ (1909) under the name "šibljak". DOING KRAFT (1955) was the first to take the latter formation into account in the frame of the Braun-Blanquet system by giving them provisionally the order name "*Cotinetalia coggygriae*". *Prunetalia* and *Cotinetalia* are deciduous shrub communities, Aestifruticeta in the sense of RÜBEL (1930). A parallel sere is formed by the two mediterranean evergreen shrub types, Durifruticeta in the sense of RÜBEL (l.c.), which were distinguished by ADAMOVIČ (l.c.) as "macchia" – in the plains – and "pseudomacchia" at somewhat higher altitudes, between macchia and šibljak. DOING KRAFT (1955) completed this system by designating the *Prunetalia* as "pseudo-šibljak".

In refining the analysis of divergent vegetation pattern MÜLLER (1962) has advanced further by resolving the old so-called "Steppenheide-problem" syntaxonomically. He described and developed a quite new class of "Hochstaudenhalden" or "Saumgesellschaften", i.e. the tall herb communities on the margins of woodland mantle, which he named *Trifolio-Geranietea sanguinei*. Along with the further refining of analysis goes a stronger accentuation of structure as a diagnostic feature. In fact, the alliances and associations all newly described by MÜLLER (l.c.) within this class *Trifolio-Geranietea* have been so faintly characterized – they hardly present any faithful or even good differential species with a comforting selectivity – that nobody would have brought them into a separate class if no structural arguments were available. This weak floristic characterization, however, has nothing to do with poverty in species: these very communities are extremely rich in species. The problem of characterization in this case is directly dependent on the vague contours within the mosaic pattern: the presence optimum, i.e. the relative accumulation of any species in a given community compared with the adjacent communities, is always small. In this case, too, the Braun-Blanquet system attains to a limit of possibility, but for just the opposite reasons from those of the case in pioneer communities. The most extreme case of a phytocenosis rich in species on a divergent habitat, where a maximal rate of energy flow within internal rhythmic dynamic processes coincides with a great stability of the ecosystem as a whole, is the tropical rain forest, where hundreds of tree species occur on a quadrat mile, and every species is represented by very few individuals. As yet, the Braun-Blanquet system is not suitable for this community type. This is, however, exceptional. As we have shown above, the increasing use of structure provides the Braun-Blanquet system with a greater flexibility and more possibilities of being applied in different ecosystem types. The most important point is the gradual shifting from dogmatism to pragmatism. We may conclude with BRAUN-BLANQUET: "There are no right and wrong systems, only good and bad ones".

5. AN ATTEMPT AT CLASSIFYING THE VEGETATION CLASSES OCCURRING IN THE NETHERLANDS INTO STRUCTURAL UNITS

5.1. *Introduction*

In the last twenty years, the Braun-Blanquet system of classification of European vegetation has considerably changed, as may have appeared in the preceding chapters. As far as I know, a completely up-to-date survey has not been published. The most recent syntaxonomic survey of the vegetation of Northwestern and central Europe (except for the alpine areas) has been published by LOHMEYER *et al.* (1962); this survey has been taken over by ELLENBERG (1963) and OBERDORFER (1964).

It seemed worth while to try to classify the units of this system into a structural classification. An attempt is presented below. For the sake of surveyability only the classes are given, as they are the highest units which have been described in this region. The author prefers to restrict himself here to Dutch vegetation. This restriction is not a big disadvantage, since the bulk of the classes of non-alpine W. and Central Europe occur in the Netherlands. As authors' names should only be added when such are desirable to avoid confusion, such names have been omitted if they are also found in the surveys of LOHMEYER *et al.* (l.c.), ELLENBERG (l.c.) and OBERDORFER (l.c.). More recent or deviating class names have been provided with their authors' names; references relating to these classes may be found in BEEFTINK (1962, 1963), DOING (1962), DOING KRAFT and WESTHOFF (1959), DEN HARTOG and SEGAL (1964), SEGAL (1965), TÜXEN and WESTHOFF (1963).

An attempt has been made to define the structural units given below in terms of spatial arrangement and life form spectra only. (Edaphical factors which are not essential for this classification are only given in brackets as an aid to better understanding). The only exception is group 2, vegetations of rocks and walls; as yet, it is not possible to define this unit otherwise than in an ecological way.

A term for the structural units presented here has been avoided. It seemed not quite appropriate to design them as "formations".

The scheme is meant to be provisional only. It might appear to be practical to lump some units (e.g. 12, 13 and 14), and to split up some others (e.g. 2, 5 and 6), to get a better-balanced system.

5.2. *Scheme of structural units with the 37 classes assigned to them*

1) Vegetations consisting of hydrophytes and amphiphytes (growing in an aquatic habitat and not or hardly emerging from it).
Classes: *Lemnetea – Charetea* (KRAUSCH, 1964) – *Potametea – Ruppietea* (J. TX., 1961) (DEN HARTOG et SEGAL, 1964) – *Zosteretea – Littorelletea.*

2) Vegetations of rocks and walls.
Class: *Asplenietea rupestris.*

3) Ephemeral vegetations with a pioneer character, consisting mainly of summer therophytes, built up from a single to many species (on open, haloid soils rich in ammonium and (or) nitrates, nearly always in convergent habitats).
Classes: *Thero-Salicornietea – Cakiletea – Bidentetea – Isoeto-Nanojuncetea – Chenopodietea – Secalinetea.*

4) Pioneer vegetations consisting mainly of rhizome geophytes and poor in species (on marine mudflats and the coastal ridge of sea dunes).
Classes: *Spartinetea – Ammophiletea.*

5) More or less open, secondary, instable vegetations, consisting of several species, mainly made up of perennial plants: chiefly hemicryptophyta rosulata, scandentia et scaposa (on more or less disturbed soils rich in nitrogen, always in convergent habitats).
Classes: *Epilobietea – Plantaginetea maioris – Artemisietea vulgaris.*

6) Communities consisting mainly of helophytes (in swamps and springs).
Classes: *Phragmitetea – Scheuchzerio-Caricetea nigrae* (syn.: *Parvo-caricetea*) – *Montio-Cardaminetea.*

7) Closed and open grassland communities consisting mainly of hemicryptophytes – the bulk of them being hemicryptophyta caespitosa –, a considerable number of therophytes – for the larger part winter annuals –, and next, if any, geophytes and chamaephytes (on dry soils and on the ecotone between dry and salt habitat).
Classes: *Sedo-Scleranthetea – Festuco-Brometea – Violetea calaminariae – Saginetea maritimae* (TÜXEN et WESTHOFF, 1963).

8) Closed (rarely open) grassland communities consisting mainly of hemicryptophytes – the bulk of them mostly hemicryptophyta caespitosa –, exceptionally mainly chamaephytes, but differing from the previous group by the smaller content or absence of therophytes (on damp to wet, fresh or salt soils).
Classes: *Molinio-Juncetea* (BRAUN-BLANQUET, 1947) – *Arrhenatheretea* – *Asteretea tripolium* (BEEFTINK et WESTHOFF, 1960).

9) Closed, sometimes more open communities of tall perennial herbs, mostly hemicryptophyta scaposa, chamaephytes and lianes; often bordering shrubs and forming an intricate mosaic pattern with shrub communities (in divergent ecocline habitat, mostly on dry calcareous soils).
Class: *Trifolio-Geranietea sanguinei.*

10) Communities of nanophanerophytes with a mostly conspicuous – sometimes predominating – layer of bryophytes: tussocks of raised bogs; heaths and moorlands.
Classes: *Ombro-Sphagnetea* – *Nardo-Callunetea.*

11) Shrubs or Fruticeta (on dry to wet soils, mostly in divergent habitats).
Classes: *Rhamno-Prunetea* (RIVAS GODAY et BORJA-CARBONELL, 1961); *Franguletea* (DOING, 1962) – *Salicetea purpureae.*

12) Poorly stratified deciduous forests (but with lianes); undergrowth poor in species, especially poor in therophytes and nanophanerophytes, but always with a certain amount of telmatophytes in the sense of IVERSEN (1936); moss layer either not very conspicuous (though often rather rich in species) or consisting of sphagnoid chamaephytes (azonal swamp woodlands and "carr" on wet peat soils).
Class: *Alnetea glutinosae.*

13) Poorly stratified deciduous forests (but with lianes); in boreal, baltic and montane Europe also acicular forests. Undergrowth poor in species, without any telmatophytes, but often with abundant or even dominant nanophanerophytes; moss layer often conspicuous (azonal woodlands on poor, very acid, dry to damp mineral soils).
Class: *Querco-Piceetea* (DOING et WESTHOFF, 1959) (syn.: *Quercetea roboris-petreae* and *Vaccinio-Piceetea* lumped together).

14) Richly stratified forests; undergrowth rich in species and consisting of many life forms, but rarely with a conspicuous amount of nanophanerophytes (zonal woodlands on rich, dry to damp, mineral soils or mineralised peat soils with a crumb structure).
Class: *Querco-Fagetea.*

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TWO QUESTIONS ABOUT MASS SELECTION IN CONNECTICUT SHADE TOBACCO

J. RIETSEMA

(*CULBRO Tobacco Division of General Cigar Co., Inc.,
West Hartford, Connecticut, U.S.A.*)

(*received November 9th, 1965*)

Connecticut Shade Tobacco is cigar wrapper tobacco. It is grown under cotton netting and hence it is referred to as "Shade Tobacco". Such tobacco is grown in Florida and in the Connecticut Valley. Many growers of Connecticut Shade Tobacco produce their own seed for future crops. They select plants in the field and, after the leaves have been picked, they harvest and bulk the seed from these plants. When a variety is not a pure line the method of plant selection for seed production can have a considerable influence on future crops. The objective of this paper is to comment on two aspects of mass selection relative to its effect on the variety when this is not a pure line.

SELECTION CRITERIA

Selection criteria fall into two broad categories: quality and yield. Although a wrapper leaf contributes only a small amount of tobacco to the cigar it has a considerable effect on smoking quality. Furthermore, it determines the appearance of the cigar. This makes *quality* very important. In the past the *yield* was often, but not always, of secondary importance, as was observed by HAYES, EAST and BEINHARD (1913). The enormous expense of growing Shade Tobacco has forced more emphasis on yield recently, and to ignore yield now would be unrealistic. Thus, tobacco growers and breeders have to pay attention to both quality and yield, and in so doing must consider a large number of characteristics. Some of the characteristics which can be observed in the field are: leaf size, shape and texture; internode length; angle of leaf with stalk; venation; number of leaves; sucker development; flowering time; plant vigor; and uniformity.

Disease resistance is important and often has to be considered in selection if not all plants possess resistance in the same degree. The more important diseases are tobacco mosaic, black root rot (*Thielavia*), blue mold, and weather fleck.

Quality traits are particularly difficult to describe and are usually impossible to measure. Some of them are taste, aroma, burn, texture and color. Although these individual aspects of quality are indeed very important breeding characteristics, they can scarcely be considered in mass selection at all. They come to full expression only after curing and fermentation, and they are not known to the selector who has to make his decision in the field. Furthermore, the ultimate quality of the tobacco is not only determined by the leaves themselves, but is strongly influenced by management practices on the farm and in the warehouse.

SEED PRODUCTION

It is relevant to our discussion to discuss the seed production process. Obviously, it is more than simply collecting a quantity of seed. In the first place, in the next generation the variety should remain unchanged and be kept 'stable'.

In the second place, it is often thought that the mass selection process might even be used to improve the variety. In such cases the borderline between mass selection for seed production and breeding for improvement becomes, then, rather vague. In practice, a 'stable' strain is a strain with little *variability*. For a commercial operator a uniform crop is of great value, because it facilitates many aspects of handling and is more profitable. It is often hoped that variability is reduced in the next generation after mass selection. Unfortunately, most Connecticut varieties are quite variable under current field management practices.

For instance, in a series of measurements undertaken on a random group of thirty plants of the variety Connecticut 49, the mean product of the length and width of the 11th leaf was 295.9 ± 41.1, or a coefficient of variation of 13.9 %. The mean length of the stalk to the 20th leaf was 60.6″ ± 5.6, or a coefficient of variation of 9.2 %.

A number of these plants were selfed and the next generation was grown. Of the next generation, the mean of the products of length and width of the 11th leaf together with the mean stalk length to the 20th leaf were determined. Again, the variability in the next generation was considerable (Table 1). This variability is phenotypic. The magnitude of the contribution of environment is unknown. That the effect of the environment can be considerable was shown by MANN and TISDALE (1956). They showed that the use of pots or separators for transplanting cigarette tobacco plants greatly reduced the variability of plant weight. Similar observations were made by us with shade tobacco by comparing plants transplanted in the regular way with plants grown and transplanted in peat pots. In one experiment the diameter at the tenth leaf level of potted plants and of regularly transplanted plants was the same, but the standard deviation of the potted plants was much lower:

3.35″ ± 0.19 for potted plants vs.
3.35″ ± 0.32 for regularly transplanted plants.

The magnitude of genotypic variability is unknown, but from experience it would also seem large. A high degree of genetic variability in Florida Shade Tobacco was noted by DEAN (1963).

Genetic variability may have several causes, even if mutations are excluded. The tobacco plant is essentially self-pollinating and produces

TABLE 1

Comparison of the means of leaf size (product of length × width of the 11th leaf and stalk length of 10 plants of the F_1 with the size (product of length × width of the 11th leaf) and stalk length of the parent plant P. All figures have been adjusted so that the column means equal 100.

Parent plant no.	Product, length × width, 11th leaf		Stalk length to 20th leaf	
	P	F_1	P	F_1
1	70	112 ± 10.6	110	112 ± 6.1
2	92	99 ± 20.1	99	107 ± 7.3
3	101	92 ± 12.8	91	98 ± 6.1
4	97	100 ± 12.8	101	99 ± 6.1
5	131	124 ± 15.2	93	104 ± 4.3
6	114	93 ± 14.3	93	112 ± 5.8
7	111	96 ± 8.1	91	86 ± 4.9
8	93	92 ± 14.1	108	95 ± 4.5
9	80	90 ± 9.5	95	94 ± 3.7
10	103	102 ± 13.5	118	92 ± 5.8
	100	100	100	100

thousands of seeds, but it outcrosses easily both naturally and artificially. In tobacco fields outcrossing can occur to a considerable extent. LITTON and STOKES (1964) found that in Burley 37 the frequency of outcrossing ranged from 1.08% to 18.95%, although in Kentucky 16 it was much less. Only when precautions are taken to prevent cross-fertilization can one be sure of complete selfing.

Before a new strain is released for commercial purposes it is usually carefully inbred for a number of generations. For instance, Round Tip was inbred for at least 10 generations prior to its release (JONES, 1921). A detailed account of the development of Burley 21 was given by HEGGESTAD *et al.* (1960), also showing a carefully controlled breeding schedule. In such cases, varieties given out to farmers are probably homogeneous and are highly homozygous.

However, because of the constant demand for new strains, it often happens that insufficient time is allowed for thorough inbreeding after the last cross or backcross, and in such cases a mixture of lines, not all homozygous, may be the result. Connecticut 49 may have been a case in point, it having been derived from a cross in 1945 (cf. SAND, 1960). It was a variable, segregating strain and it was possible to derive from it a number of very different lines that were hardly recognizable as members of the same family. Another example was the strain BR 13. This does not mean that all varieties of shade tobacco are this variable. Some existing strains, such as General Cigar's # 396 and # 911, are more uniform.

MASS SELECTION METHODS

There are several possible methods of producing seed from an established variety. The easiest manner of seed collecting would be taking of seed from a number of arbitrary plants and subsequently mixing it into a seed batch. This is rarely, if ever, done.

Another simple method would be to block off a certain portion of a field and to save the seed of all plants. A small refinement would be to eliminate obviously poor plants. This method is still practiced today. In the fall, the traveler through the Connecticut Valley can still find an occasional field with all tobacco cut, but with a dozen or so plants standing in a row and allowed to go to seed. This refers more to Havana Seed, a binder type, than to shade tobacco where this practice is perhaps only occasionally followed.

Still another method is to make a careful selection and to allow only superior plants to contribute to the seed harvest. This selection method is often used. When disease resistance is involved, the flower heads are bagged to prevent cross-pollination from other plants. Regarding the choice of field, it is believed by some that plants from outstanding fields produce better offspring than plants from poorer fields. Thus, great attention would be paid to the choice of the field from which to select seed plants.

Regarding the merits of these methods of seed production, two questions arise in the case of varieties which are not homozygous and homogeneous.

1) To what extent can these procedures be expected to keep an existing variety constant?

2) To what extent can selection pressure applied in mass selection lead to improvements in the variety?

1. GENOTYPE OF THE NEXT GENERATION

To answer the first of the preceding questions, viz., to what degree does the next generation reproduce the parent generation, is relatively simple for an idealized situation, provided we make certain assumptions:

1) All plants produce the same number of seeds and the seeds have the same viability. Although this is never so, it may be assumed when dealing with large numbers of selected plants.
2) Use only large populations and large samples. This is nearly always the case.
3) Disregard mutations and linkage.
4) Tobacco behaves as a regular diploid. This is probably true as long as one may disregard the products of inter-specific hybridization (see GOODSPEED, 1954).

Starting with a population from which a large random sample is taken for seed production, it is further assumed that the genotypic array of the sample is very similar to that of the population as a whole. In the case of self-fertilization for one locus with two alleles:

Genotypic array parent:

$$p^2AA + 2pq\,Aa + q^2aa, p + q = 1.$$

Genotypic array F_1:

$$(p^2 + \tfrac{1}{2}pq)AA + pq\,Aa + (q^2 + \tfrac{1}{2}pq)aa.$$

As the proportion of heterozygous plants decreases, the proportion of homozygous plants increases correspondingly. It is immediately obvious that the degree of change is greatest when $p = q$ and least when p or q are close to 1. Ultimately, the heterozygotes disappear altogether and fixation of characters occurs. The population becomes stable, and further selfing will not change its composition. The rate of fixation is given by the general expression:

$$(p^2 + F_n\,pq)AA + 2(1 - F_n)pq\,Aa + (q^2 + F_n\,pq)aa$$

where F_n is the coefficient of inbreeding after n generations (see FALCONER, 1964, p. 65). To determine how the changes in genotypic array influence the mean value of the population in the next generation, and assuming no over-dominance, assign the values y toAA, $\frac{1}{2}(y - x)$ to Aa and 0 to aa and obtain:

Parent: $py - pqx$

F_1: $py - \frac{1}{2}pqx$

The mean value of the population for this character changed in the next generation with $\frac{1}{2}\,pqx$. Idealized as this model is, it does indicate that without selection the next generation of plants differs from the parent populations in genotypic array and mean value for any one attribute. It further indicates that unless complete homozygosis exists the seed producer should not expect his new seed to be the same as his old if his selected plants are a random sample. However, when one deals with a highly inbred variety this effect is far less important than in cases where p is close to $\frac{1}{2}$.

In the case of selection pressure against one of the genotypes, a model can once again help to understand the results. Obviously, if homozygotes are favored, say AA and aa over Aa, homozygosity will be reached sooner. If, on the other hand, heterozygotes are favored, and hence homozygotes are at a disadvantage, homozygosity may never be reached. In a field, when there is no distinction among lines and where selection is within and between lines simultaneously, the distribution of genotypes can be predicted according to the formulas of HALDANE (1956). Assigning to the relative fitnesses of AA, aa and Aa the values 1–k, 1–1 and 1 respectively, and to the parent generation the array $p^2\,AA + 2pq\,Aa + q^2\,aa$ we obtain after Haldane for the next generation:

$$AA:\quad (1 - k)\,(p^2 + \tfrac{1}{2}pq)/1 - k(p^2 + \tfrac{1}{2}pq) - l(q^2 + \tfrac{1}{2}pq)$$

$$Aa:\quad pq/1 - k(p^2 + \tfrac{1}{2}pq) - l(q^2 + \tfrac{1}{2}pq)$$

$$aa:\quad (1 - l)\,(q^2 + \tfrac{1}{2}pq)/1 - k(p^2 + \tfrac{1}{2}pq) - l(q^2 + \tfrac{1}{2}pq)$$

Equilibrium is reached when for Aa:

$$2pq = pq/1 - k(p^2 + \frac{1}{2}pq) - l(q^2 + \frac{1}{2}pq).$$

In other words, conditions might be such that complete homozygosity is never reached. It depends on the magnitudes of k, 1 and p whether equilibrium will be reached with a certain percentage of heterozygotes, or only after complete fixation. In most cases, when starting with a heterozygous population with p near ½, the next generation will be different from the parent generation, the extent of difference being determined by the degree of disadvantage of one genotype over another. A situation as just described could be envisaged for tobacco if hybrid vigor would occur (see SMITH, 1952). The model can be extended to more alleles for each locus and to more loci.

Outcrossing has been disregarded in the previous models. Should outcrossing occur, it would be impossible to predict the genotypic composition of the next generation except in very general terms. Natural outcrossing depends on climate, insects, location and proximity to other tobacco fields, and it can assume considerable proportions. Selection efforts could be largely wasted if no measures were taken to prevent unwanted hybridization.

What has been said so far shows that there is a very good chance of not reproducing a particular seed lot, unless outcrossing is prevented and the parent population represents an already homozygous line. Also, it can be expected that the greater the degree of inbreeding, the smaller the changes in the next generation.

2. PHENOTYPE VERSUS GENOTYPE: IMPROVEMENTS

The real difficulty in a field of tobacco is to recognize the desirable genotypes from among a population of phenotypes. In the event of several fields with plants of the same variety and from the same seed lot, an additional choice of field has to be made. The problems are by no means new, and the theory of selection offers some guidance in their solution.

First, it must be recognized that only in the case of quantitative characters are these problems relevant. For characters such as disease resistance and flower color, selection usually does not offer great difficulties. As we have seen, however, most of the important attributes are of a quantitative nature. How much a variety can be improved by mass selection can be determined by means of *selection response* (see FALCONER, 1964, Ch. 11). With one locus, and only 2 alleles, the actual gain after selection can be measured by the difference between the population mean and the mean of the offspring of the selected individuals. It can be expressed as:

$$R = i\,\sigma_p\,h^2$$

R = selection response
i = intensity of selection
σ = standard deviation in phenotypic value
h^2 = heritability of attribute

The intensity of selection 'i' equals D/σ_p, where D is the selection differential, and σ_p the standard deviation in phenotypic value. This value can be computed from the formula of the normal distribution curve, and depends on the inverse of the proportion of selected individuals to total population. Hence, response R can be increased by lowering the percentage of selected individuals, or by increasing the heritability which becomes greater when the phenotypic standard deviation decreases. As KEMPTHORNE (1957) pointed out, however, this response can only be predicted if the gene effects are additive. Indications are that much of the genotypic variance is of an additive character (LEGG *et al.*, 1965) (MURTY *et al.*, 1962). Assuming that the restriction holds for shade tobacco as well, and returning to the tobacco field, the greatest response could be expected with a small number of selected plants, and the greatest possible uniformity in growth and development.

So far, we have considered only one locus. As soon as selection is made for a combination of attributes, the situation immediately becomes more complex. This is precisely the problem with mass selection. In selecting seed plants for future crops, the entire plant is judged on the merits of a number of attributes at the same time, although usually no precise information is available on whether or not these attributes are correlated. A plant is given a 'value' in comparison with the 'mean' value of the field. The words 'value' and 'mean' are now used loosely because, as a rule, actual measurements are not made. This total 'value', or selection index, is actually compound and made up of a number of weighted attributes. Furthermore, the value of each attribute consists of the sum of the genotypic value G and environmental value E. We can only learn something about the phenotypic value P and have to estimate G from P. This can be done provided variances, co-variances, and certain other parameters are known (HAZEL, 1943).

In practice, however, such a selection index cannot be used for mass selection when considering a great many individuals and a substantial number of characters. But, at least in theory, progress can be made by selection based on measurement, even if involved with many characters at the same time. Since usually we have no idea of the 'value' of a plant, selection for a number of characters at the same time remains guesswork and strictly subjective.

We may now consider the next question: Which field should be used for seed selection if a selection pressure is applied? If selections are made from a very good field, will the next generation produce as well on a poor field? Or are the better plants from a very poor stand the same plants that would be outstanding if the field were above average? By regarding the performance in different fields as the result of different characters, it is possible to obtain an idea of the so-called correlation response between these characters. FALCONER (1964) explains that when the correlation is high, the same genes control performance in different environments. Hence, it would make little difference in what environment the selections are made. If the correlation is low, it would be better to select in the environment where the population is expected to grow. For shade tobacco we do not have information on these correlated responses. Experience seems to indicate that with the low selection intensity usually applied, the field has little or no effect on the next generation. This is not really surprising. However, if the selection were severe and the intensity high, the population environment might make a difference. This possibility would have to be demonstrated and cannot be assumed.

It is clear that it is almost impossible to predict a response to mass selection when many factors remain unknown.

SUMMARY

From the general discussion of the effect of mass selection on the genotypic array of the next generation we have seen that under certain conditions mass selection can lead to homozygosity, but does not do so necessarily. Outcrossing, mutations and disadvantages of certain genotypes may prevent reaching equilibrium condition with complete homozygosity even in the simplest case of one locus with two alleles. It depends on the magnitude of these factors and the degree of heterozygosity of the variety how close to genetic uniformity we ultimately can come. The advancing of one generation has only a small effect, which becomes less as the frequency of one of the genotypes becomes less. Mass selection can reduce segregation in a variety, but only in ideal situations and only in small steps. Obviously the most effective way to promote genetic uniformity is to begin with non-segregating material obtained through careful inbreeding and within-family selection. Then, if this is available, mass selection is hardly necessary and seed collection should be done so as to prevent a return to a heterozygous condition. When only segregating populations are available, some changes can be expected if the selection intensity is low, but they will not be great and may not be noticed until after several generations.

Returning to the original question of the stability of the tobacco variety, the conclusion can be drawn that when large numbers of plants from a field are selected as seedplants the changes in the next generation as a whole will be small, regardless of the selection procedure used. When 10–30 % of all plants are allowed to produce seed we cannot expect important changes. Also, when the environmental variations are as great as in shade tobacco, the possibilities of selecting against certain genotypes for a number of characteristics simultaneously becomes virtually impossible.

Concerning whether or not mass selection can lead to improvements in the variety, it was explained that the selection intensity and the heritability of a character determine the selection response. Perhaps this response can be predicted in the case of one character, but it becomes difficult, if not impossible, to forecast the results when many characters are involved at the same time. Reference was also made to a selection index which has been effective in livestock breeding. Even if an index could be determined for shade tobacco, its use is not necessarily effective, as KEMPTHORNE (1957) pointed out. The genotype-environment interaction makes questionable the choice of certain fields over others. Without experiments, such questions cannot be answered. It is likely that mass selection with low selection pressure changes a variety very little. Again, in a field where up to 30 % of the plants are selected for seed, the pressure cannot be very great and we should not expect great changes. Only when a few plants are carefully selected for certain characters should progress become noticeable, as is the experience of single plant selection in plant breeding.

We conclude that mass selection for seed and plant breeding to improve a variety should not be confused with each other. Each has its own aims and methods, which are not interchangeable. Where uncertainty exists about seed, progeny tests usually are made to compare a seed with the parent seed. BOLSUNOV (1959) has described a number of such procedures for tobacco, though the more elaborate of them appear impractical.

ACKNOWLEDGMENT

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DORATOMYCES COLUMNARIS SP. NOV.

H. J. SWART

(*Department of Botany, University of the Witwatersrand, Johannesburg, South Africa* [1])

(*received November 1st, 1965*)

In the course of a routine investigation of fungi growing on dung pellets of hares collected in the Melville Koppies Nature Reserve in Johannesburg some rather small coremia were noticed. Slides were prepared and an attempt made to isolate the organism in pure culture was successful. The structure of the coremium appeared to be the same as in the genera *Doratomyces* (Morton and Smith, 1963) and *Trichurus* (Swart, 1964), and in addition the conidia were seen to occur in chains on annellophores. No setae were present and therefore the organism was classified as a species of *Doratomyces*, however it did not fit the description of any of the species as summarised by Morton and Smith (1963), for this reason the organism is described here as a new species. The description is based on the study of the original material and of material from cultures on oatmeal decoction agar and oatmeal-dung extract agar.

Doratomyces columnaris H. J. Swart, sp. nov.

Coremia sunt parva, raro plus quam 50 μ alta, quae caput parvum et supra paene aequum habent; annellophora 6–10 μ alta, basi tumefacta 2–3.5 μ diam., quae in zonam annellatam, 1.75–2.25 μ diam., praerupte fastigata sunt; conidia sunt levia, basi truncata et cacumine plerumque acuto ovata, 6(4.5–8) × 3.5 (3–4) μ, et cinerea aut etiam nigra universa, quae in vinculis cohaerent et columnam summo coremio efficiunt.

Coremia small, rarely more than 50 μ high, bearing an almost flat topped small head; annellophores 6–10 μ long with swollen base 2–3.5 μ diam., tapering abruptly into the annellated zone 1.75–2.25 μ diam.; conidia smooth, ovate with truncate base and usually distinctly pointed apex, 6 (4.5–8) × 3.5 (3–4) μ, dark grey to black in mass, produced in chains which adhere to form a column on top of the coremium.

Growth in agar culture is rather fast; coremia form a dense stand in which individual ones cannot be distinguished; smaller conidiophores are abundant.

The coremia follow the pattern established by Morton and Smith (1963). The downward growing branches are limited in number

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[1] Present address: School of Botany, University of Melbourne, Victoria, Australia.

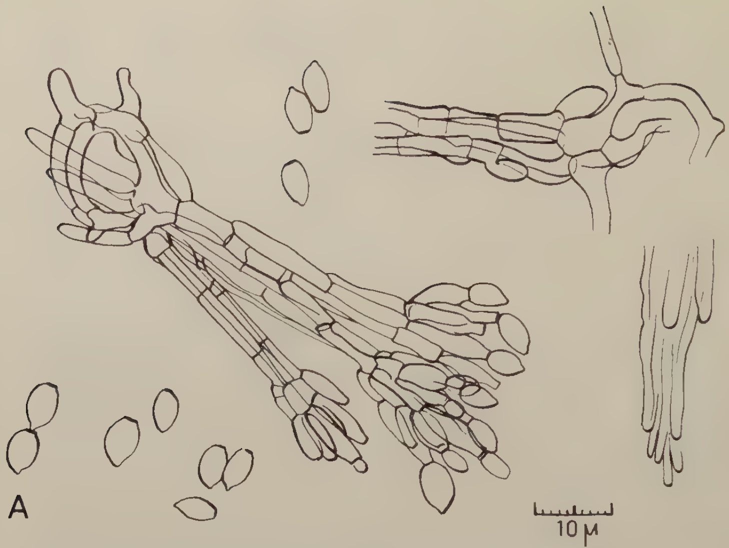
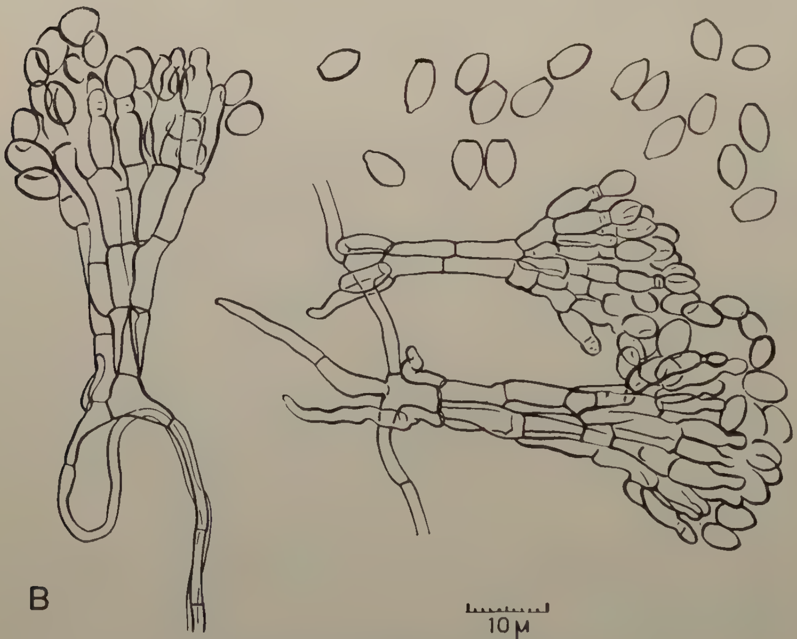


Fig. 1. Details of coremia and conidia of Doratomyces columnaris. A: from dung;



B: from agar culture. Scale 10 μ.

and arise from the lower part of the coremium. In several cases coremia have been seen to arise from a hyphal coil. The coremium often arises from a distinct basal cell in the mycelium, occasionally two such cells can be seen at the base of a single coremium.

The main characteristic features of the species are the very short coremium topped by a small almost flat head from which the conidia arise in a column.

Cultures of the type strain have been deposited at the C.M.I., Kew, and the C.B.S., Baarn.

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MOSSES FROM THE NETHERLANDS ANTILLES

P. A. FLORSCHÜTZ
(*Botanical Museum and Herbarium, Utrecht*)

(*received December 1st, 1965*)

The Netherlands Antilles comprise the islands Aruba, Curaçao and Bonaire of the Leeward Group, and St. Eustatius, Saba and the southern part of St. Martin (St. Maarten) of the Windward Group. The northern part of St. Martin belongs to the French territory (Département de la Guadeloupe).

Botanical investigations were started already in the 18th century, but it was not before 1909 that an enumeration of the vascular plants of part of the Netherlands Antilles appeared in print (Boldingh, 1909; the other part appeared in 1914). In 1913 Boldingh published a Flora of the Netherlands Antilles (in Dutch). Brother M. Arnoldo published a Flora of Curaçao, Aruba and Bonaire (in Dutch, 1954; second edition 1964). An elaborate study of the vegetation of the islands was published by Stoffers (1956). Some of the data given below are borrowed from that paper. A new Flora is now in the course of publication (edited by Stoffers since 1962).

In spite of all these botanical investigations it seems that nothing has been published on the bryophytes of the islands. In this paper I have listed a number of mosses collected in recent years. Of the collectors mentioned by Stoffers (l.c.) the following persons also collected bryophytes:
W. F. R. Suringar, 1885; his collections are in the Rijksherbarium, Leiden. As already said for the Suriname collections made by Suringar (Florschütz, 1964), his specimens have been named by v. d. Sande Lacoste and, without being published, have been inserted under those names. In due time they will have to be selected by going through all South American mosses at Leiden. A few specimens were met with accidentally and these are listed below.
P. Wagenaar Hummelinck, 1937, 1949, 1955.
Brother M. Arnoldo, since 1945.
A. C. J. Burgers, 1948.
A. L. Stoffers, 1952–'53 and 1963.
Finally I collected a few specimens during a one-day trip to the Christoffelberg in Curaçao in 1965. Apart from those collected by Suringar, all specimens are in the Utrecht Herbarium.

The mossflora of the Leeward Group is very poor. The climate is relatively dry, the mean rainfall during a year being 359 mm in Aruba, 525 mm in Bonaire and 516 mm in Curaçao. It seems that no mosses have been collected in Aruba. It is by far the driest island and there are no high hilltops, the highest elevation being 188 m. Although the rainfall in Bonaire is distinctly higher than in Aruba, only 3 mosses, *Hyophila microcarpa*, *H. tortula* and *Gymnostomiella orcuttii*, have been collected in this island up till now. The lack of real forest possibly prevents the establishment of more moisture-loving species in this island. From Curaçao 6 species are listed below, five of which have been collected on the highest hill (Christoffelberg, 372 m) in the western part of the island with a relatively luxuriant forest vegetation. In the lower parts of this island only *Hyophila microcarpa* is met with occasionally.

The Windward islands Saba and St. Eustatius have by far the richest bryoflora of the Netherlands Antilles. This is mainly due to the higher elevation (St. Eustatius 600 m and Saba 900 m) and to the higher rainfall (mean rainfall during a year 1110 and 1133 mm respectively for the lowlands; on top of the mountains probably more than 2000 mm). According to Stoffers an elfin woodland (mossy forest) is to be found on the highest parts of these islands. St. Martin, on the contrary, is very poor in mosses. Although the rainfall is nearly as high as in Saba and St. Eustatius (1027 mm) the highest elevation is only 400 m and real forest is not present. Only 2 species, i.e. *Stereophyllum cultelliforme* and *Hyophila tortula* have been collected in the French part, just across the border. From Saba 17 species are mentioned and from St. Eustatius 13 species are known. Although most of the moss species mentioned below are widely distributed in the Caribbean area and beyond, it is curious that these two islands, only about 30 km apart, have only 3 species, i.e. *Hyophila tortula*, *Trichostomum jamaicense* and *Acroporium pungens*, in common. The vascular plant vegetation as described by Stoffers is indeed different, but ecological circumstances do not seem to differ to such an extent that common tropical American mosses, such as *Groutiella mucronifolia*, *Meteoriopsis remotifolia*, *Neckeropsis undulata* and *Orthostichopsis tetragona*, will not find a suitable habitat for establishment in both these islands. Probably more intensive moss-collecting in the islands will reduce these differences.

As already said above, most of the species mentioned in this paper are widely distributed over tropical America, one third of the total number even ranging from the Southern United States via the West Indies, Mexico and Central America to tropical South America. Only a few species are recorded here for the first time outside their known area. *Campylopus trachyblepharon* was hitherto only known from Brazil and British Guiana. A new variety of *C. atratus* Broth. (var. *sabaensis*) is described below. The typical variety has been collected only once on Mount Roraima in British Guiana. Although *Syrrhopodon incompletus* var. *incompletus* has a very wide distribution in tropical America, its var. *luridus* has thus far been found only in the Guianas. For *Clasmatodon parvulus* this is the first record outside the North American mainland (apart from one locality in Europe).

FISSIDENTACEAE

Fissidens elegans Brid. (syn. *F. guianensis* Mont.) CURAÇAO: Arnoldo 2215A, Stoffers s.n., Florschütz 3459, Christoffelberg, on decaying wood. In my recent paper (FLORSCHÜTZ, 1964) I excluded this name from the Suriname flora because of the fact that the isotypes I had seen belonged to two different species. After the paper had been printed I was able to examine the holotype from the Bridel herbarium in Berlin. It consists of two plants (see fig. 1) and these plants are identical with *F. guianensis*. The latter name will have to be replaced by *F. elegans*. It is clear that the use of the name *F. elegans* for *F. intermedius* (as done in so many bryological papers) is incorrect.

Fissidens kegelianus C. M. CURAÇAO: Florschütz 3458, Christoffelberg, on soil.

DICRANACEAE

Campylopus atratus Broth., not Bartr. var. **sabaensis** Florsch. var. nov.

A varietate typica differt foliis siccitatis adpressis, dimidio brevioribus, 4 mm longis, minus subtubulosis. SABA: Arnoldo 3354A, The Mountain, top, ca. 900 m (type specimen, U). The typical variety has been collected only on top of Mount Roraima, British Guiana. It is very easy to know by the leafcells with thick, strongly pitted walls even at extreme apex, together with the hyaline hairpoint. This new variety has shorter leaves, only about 4 mm long, strongly appressed to the stem when dry and less subtubulose than in the typical variety.

Campylopus trachyblepharon (C.M.) Mitt. SABA: Arnoldo 3353B, 3354D, The Mountain, top; Stoffers 3463A, The Mountain, top, 825 m, epiphyte. This seems to be the first record outside the South American mainland.

LEUCOBRYACEAE

Leucobryum albidum (Brid.) Lindb. ST. EUSTATIUS: Stoffers 3681, 3698A, The Quill, top, 350–400 m; Stoffers 3956, The Quill, top, 400–480 m, on rocks; Burgers s.n., The Quill. As already pointed out by BARTRAM (1949) the differences between *L. albidum* and *L. polakowskyi* (C.M.) Card. are very slight and not convincing.

Octoblepharum albidum Hedw. CURAÇAO: Burgers s.n., Stoffers s.n., Florschütz 3453, Christoffelberg. ST EUSTATIUS: Arnoldo 3210A, The Quill, 500 m.

Octoblepharum pulvinatum (Dozy et Molk.) Mitt. ST. EUSTATIUS: Stoffers 3698B, The Quill, top, 350–400 m, epiphyte.

CALYMPERACEAE

Calymperes donnellii Aust. ST. EUSTATIUS: Stoffers 3597, The Quill, top at side of Glass Bottle, 380–400; Arnoldo 3212, The Quill, top, 500 m.

Calymperes richardii C.M. CURAÇAO: Stoffers s.n., Knip-hills, on stone wall; Florschütz 3455, Christoffelberg, on soil. SABA: Stoffers 4328, Windwardside, on wall, 400 m.

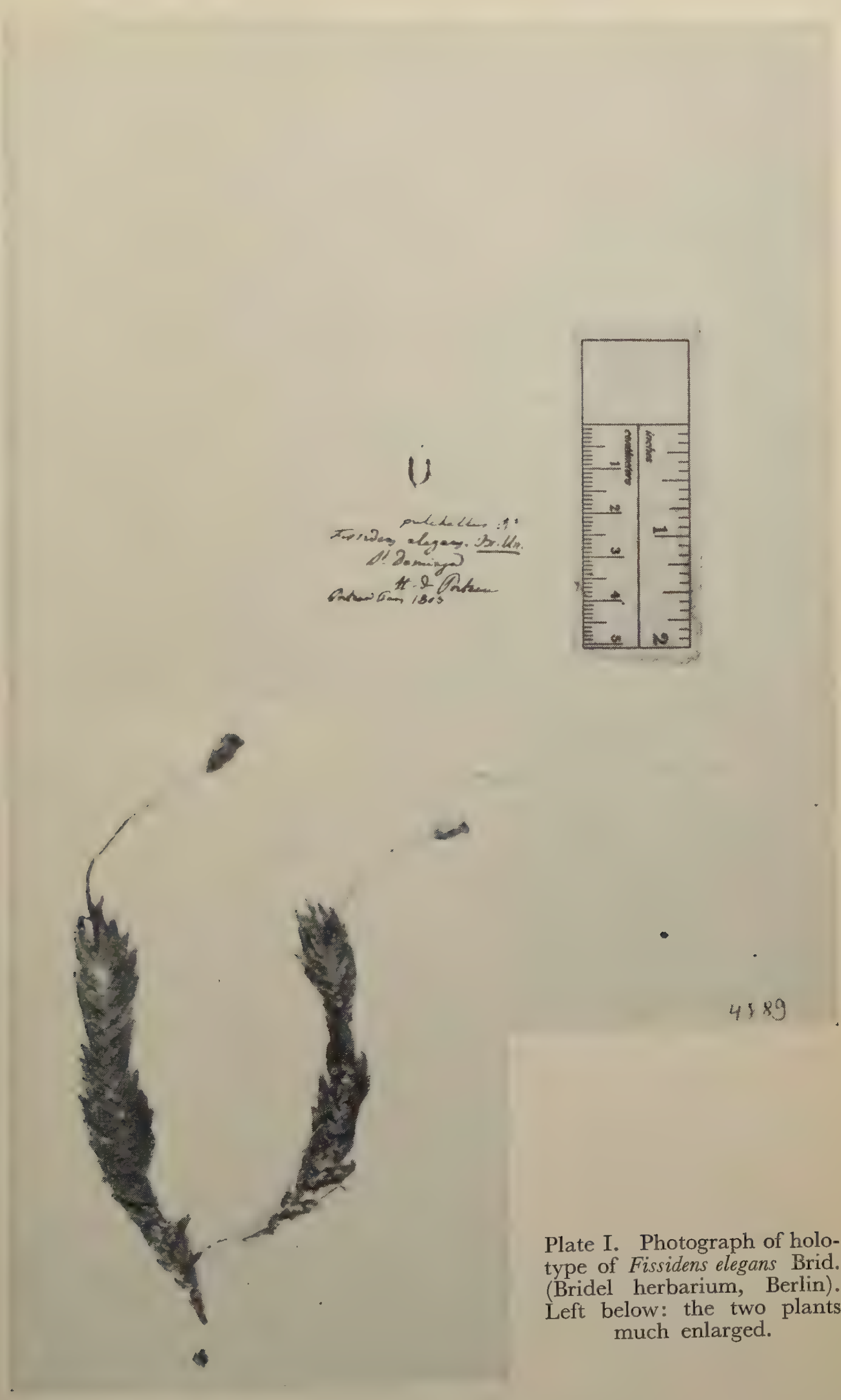

Plate I. Photograph of holotype of *Fissidens elegans* Brid. (Bridel herbarium, Berlin). Left below: the two plants much enlarged.

Syrrhopodon incompletus Schwaegr. var. *incompletus*. ST. EUSTATIUS: Arnoldo 3207, 3210, The Quill, 500 m. – var. *luridus* (Par. et Broth.) Florsch. ST. EUSTATIUS: Stoffers 3698, The Quill, top, 350–400 m, epiphyte.

POTTIACEAE

Barbula agraria Hedw. ST. EUSTATIUS: Suringar s.n., between village and The Quill.

Gymnostomiella orcuttii Bartr. BONAIRE: Wagenaar Hummelinck 188B, Spelonk, calcareous rock, shade.

Hyophila microcarpa (Schimp.) Broth. BONAIRE: Stoffers 753, Slagbaai Plantage, Hoge weg; Stoffers 834, Angola, 50 m; Stoffers 923, Seroe Grandi, 100–115 m; Stoffers 1046, Seroe Grandi, top, 200 m; Stoffers s.n., Brandaris. CURAÇAO: Arnoldo 2213, Christoffelberg; Stoffers s.n., Ronde Klip, north escarpment, calcareous soil; Stoffers s.n., Ronde Klip, north slope, calcareous soil on top of diabase; Stoffers s.n., Jan Thiel; Stoffers s.n., Knip-hills; Florschütz 3454, Christoffelberg, on soil. SABA: Arnoldo 3276, Boobyhill, 600 m.

Hyophila tortula (Schwaegr.) Hampe. BONAIRE: Wagenaar Hummelinck 48A, Fontein hofje, calcareous rock. SABA: Arnoldo 3275, Boobyhill, 600 m. ST. EUSTATIUS: Suringar s.n., between village and The Quill. ST. MARTIN: Wagenaar Hummelinck s.n., Colombier Valley, calcareous rock.

Trichostomum jamaicense (Mitt.) Jaeg. SABA: Arnoldo 3345, The Mountain. ST. EUSTATIUS: Burgers 190, The Quill, in crater.

BARTRAMIACEAE

Philonotis uncinata (Schwaegr.) Brid. var. *glaucescens* (Hornsch.) Florsch. CURAÇAO: Arnoldo 2215, Stoffers s.n., Christoffelberg.

ORTHOTRICHACEAE

Groutiella mucronifolia (Hook. et Grev.) Crum et Steere. SABA: Stoffers 4342, 4352, Santa Cruz, 500–600 m; Arnoldo 3355, The Mountain.

Macromitrium cirrosum (Hedw.) Brid. SABA: Arnoldo 3355A and s.n., The Mountain.

Macromitrium schwaneckeanum Hampe. SABA: Arnoldo 3354B, The Mountain, top.

Macromitrium scoparium Mitt. SABA: Arnoldo 3353, The Mountain, top; Stoffers 3468, The Mountain, top, 825 m, epiphyte.

PTEROBRYACEAE

Orthostichopsis tetragona (Hedw.) Broth. ST. EUSTATIUS: Burgers s.n., The Quill; Stoffers 3682, 3688, The Quill, top, 350–400 m, epiphyte.

Pireella pohlii (Schwaegr.) Card. ST. EUSTATIUS: Arnoldo 3208, The Quill, 500 m.

METEORIACEAE

Meteoriopsis remotifolia (C.M.) Broth. SABA: Arnoldo 3343, 3352, s.n., The Mountain, on tree; Stoffers 3223, The Mountain, slope under the Cliff, 680 m; Stoffers 4630, The Mountain, top, 800 m.

Squamidium nigricans (Hook.) Broth. SABA: Arnoldo s.n., The Mountain.

NECKERACEAE

Neckeropsis undulata (Hedw.) Reichardt. ST. EUSTATIUS: Arnoldo 3209, The Quill, 500 m.

Porotrichum insularum Mitt. SABA: Suringar s.n., The Mountain; Stoffers 3463A, The Mountain, top, 825 m.

HOOKERIACEAE

Lepidopilum radicale Mitt. SABA: Suringar s.n., The Mountain, 600–800 m; Arnoldo 3347A and s.n., The Mountain, on tree.

FABRONIACEAE

Clasmatodon parvulus (Hampe) Sull. SABA: Arnoldo 3346A, The Mountain. Apart from one locality in Europe, this seems to be the first record outside the North American mainland.

PLAGIOTHECIACEAE

Stereophyllum cultelliforme (Sull.) Mitt. ST. MARTIN: Wagenaar Hummelinck s.n., Colombier Valley, calcareous rock.

SEMATOPHYLLACEAE

Acroporium pungens (Hedw.) Broth. SABA: Arnoldo 3342, 3346B, The Mountain. ST. EUSTATIUS: Stoffers 3963, The Quill, top, 400–480 m.

Sematophyllum caespitosum (Hedw.) Mitt. SABA: Stoffers 4328A, Windwardside, on wall, 400 m; Stoffers 4352, Santa Cruz, 500–600 m.

ACKNOWLEDGMENT

I am much indebted to Mrs. M. M. Soekarjo for her revision of the English text.

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4.4. *Water content of the soil*

A frequent and regular measuring of the water content of the soil was impossible. Firstly these locations are situated too far from each other and secondly, the stay in Curaçao was interrupted by a trip to the island of Bonaire. However, a good impression is given by the data collected near Janwé and at Noordkant Plantation. These measurements were made on the same day at 5 and 25 cm depths at 5 days intervals during the end of the rainy season. The electrical resistance (in Ohms) between the electrodes in the plasterblocks is given in Fig. 6.

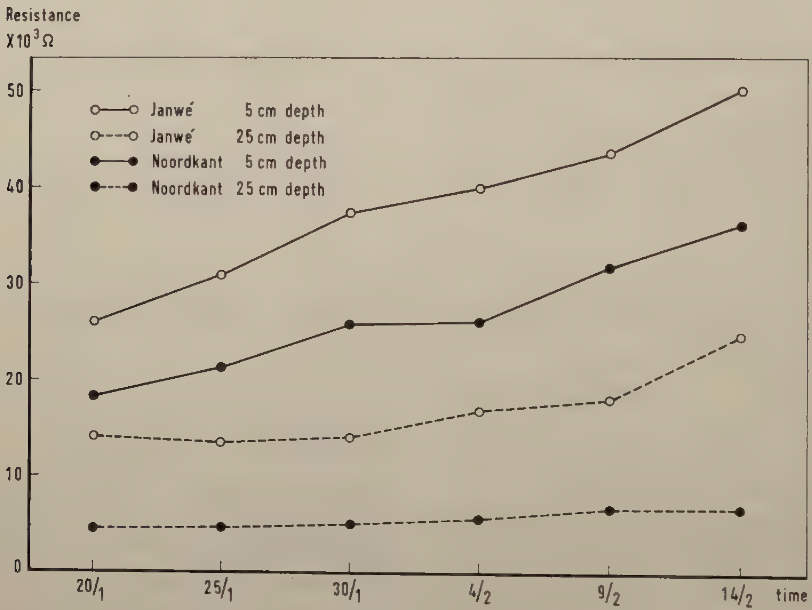

Fig. 6. Soil moisture; data obtained by the modified Bouyoucos-method. Resistance given in Ohms.

These data are mean values of three measurings. From the data it is clear that at this time of the year the limestone soil below 25 cm depth is moister than the diabase soil. Differences are smaller at 5 cm depth. It must be emphasized that water relations may shift strongly in the course of the year, as is shown by data collected in the island of Bonaire during the rainy season.

5. Discussion

If the data presented here are overlooked, then a marked difference in the water relation between plants growing on diabase and limestone becomes evident. In the first place this difference is seen in transpiration. The three types in the transpiration curves seen, reflect

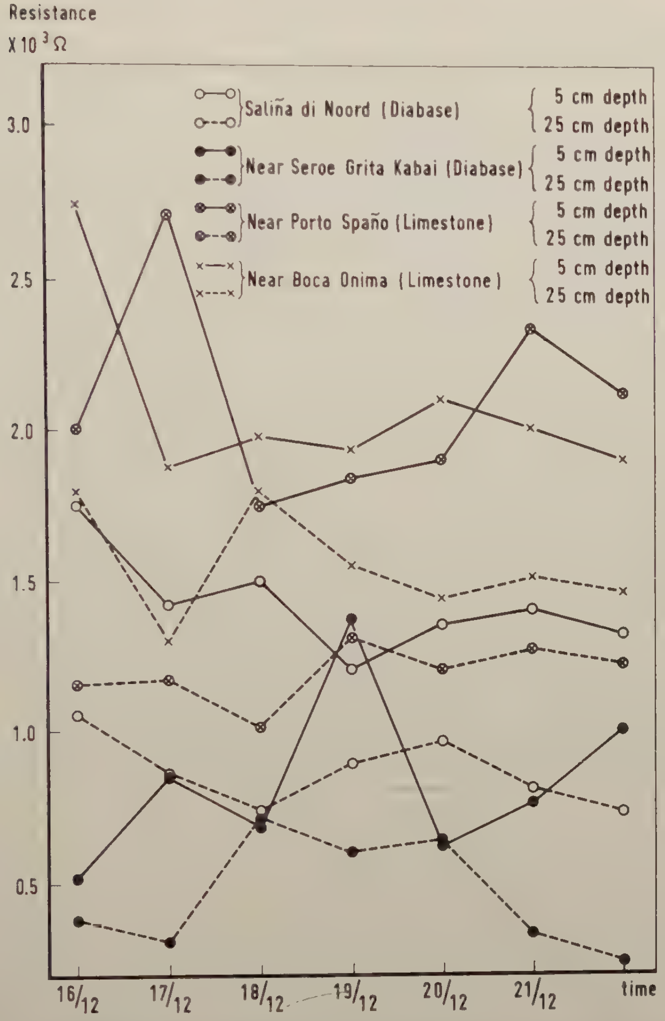

Fig. 7. Soil moisture data obtained in the island of Bonaire. Resistance given in Ohms.

clearly the water relation in the soil. If the amount of soil water is adequate the transpiration curve runs parallel to the evaporation curve (STOCKER, 1956). This is the case with *Croton flavens* growing on limestone. If this species occurs on diabase then the rate of transpiration decreases after reaching the maximum disproportionate to the decrease in evaporation. This implies that in the soil, the water supply is impeded and the water relation becomes more severe. However it is remarkable that for *Croton flavens* growing on diabase the transpiration maximum is higher than that on limestone. This could be explained either by a capability of *Croton* to develop and

This aspect is generally found in areas that are slightly wet or in which underground water is available. They are therefore often well represented along gulleys, seepage slopes and swampy plateaus. In this type of vegetation the treeferns play a dominant role and locally form transitional stages towards the closed shrubberies.

2. The aspect with low grasses also covers a large area and is mainly restricted to the drier slopes. They include a small number of grasses like *Danthonia archboldii* Hitchc. and *Agrostis reinwardtii* van Hall but usually the herbs outnumber them. Locally even no grasses at all are found. The vegetation, as in the first aspect, is composed of three layers, the highest about 50 cm tall, the second up to about 20 cm and finally the groundlevel composed mainly of mosses, lichens and such creeping herbs like *Geranium potentilloides* L' Hérit., *Hypericum japonicum* Thbg and *Oreobolus ambiguus* Kük. and van Steenis.

In this aspect the most striking species in the upper level are *Gaultheria mundula* F. Muell., *Hypericum macgregorii* F. Muell., *Styphelia suaveolens* (Hook. f.) Wbg and *Tetramolopium flaccidum* Mattf.

In the middle level *Brachycoma papuana* Mattf. is a striking but rare species, while *Cerastium papuanum* Mattf., *Epilobium keysseri* Diels and *Trachymene adenodes* Buw. are more common.

In the ground level the most striking species are species of *Gnaphalium* and *Trachymene rosulans* (Danser) Buw., together with such inconspicuous plants as species of *Haloragis* and *Anotis*.

3. The lichen aspect is a distinct one and is mainly found on dry hillocks, along forests' edges and on roadsides. The main components are species of *Cladonia* with scattered specimens of *Coprosma archboldiana* M. and P., *Cotula leptoloba* Mattf., *Gaultheria mundula* F. Muell., *Gentiana macgregorii* Hemsley, *Lactuca umbellata* Mattf. and the silvery white cushions of several species of *Gnaphalium*. Low creeping *Vaccinium* species form dense mats.

4. Is the third aspect relatively small in size, more extensive is the *Eurya brassii* aspect. This small shrub with obovate, leathery, dark green leaves is subglobose in shape in the lower areas, but becomes increasingly more depressed in the higher altitudes and ultimately forms a hard, dense mat. In this mat several species of *Coprosma* and *Vaccinium* are growing together with *Gaultheria mundula* F. Muell, but usually the number of species is very limited. The aspect if often limited to dry, exposed summits and is one of the few that reaches to near the summit area up to 4100 m.

5. The screes are not extensively developed in the Mount Biota area. This is mainly due to the harder, schistic nature of the rocks of the range and its gradual slopes. Where they are developed they are mostly completely overgrown with a low vegetation of *Centrolepis philippinensis* Merr., *Oreobolus ambiguus* Kük. and van Steenis, *Plantago lanigera* Hook. f. and *P. depauperata* M. and P. in the ground layer, while and indistinct second layer of *Drimys sp.*, *Gaultheria mundula*

F. Muell., *Hypericum macgregorii* F. Muell. and *Styphelia suaveolens* (Hook. f.) Wbg, with scattered species of *Rhododendron* and *Vaccinium*, can sometimes be recognised. The most striking species found here was *Agapetes costata* C. H. Wright recognisable by its long, pale green purple flowers.

b. WET GRASSLANDS

The wet grasslands are smaller in size than the dry grasslands but have a richer, more varied vegetation. They are found in gulleys and on flat areas on top of hills, and range from superficially wet to alpine bogs, swamps, ponds, and tarns. The number of grasses is usually rather small, the herbs dominating in these grasslands, sometimes to the exclusion of grasses. This is particularly clear on the seepage slopes and on tracks across the area.

6. In these wet areas the largest aspect is the *Oreobolus* aspect in which most of the grasses occur. This aspect is often found on wet slopes in shallow dips. It is a rather dense vegetation composed on two distinct layers. In the upper layer *Tetramolopium alinae* (F. Muell.) Mattf., grasses and *Gaultheria mundula* F. Muell are the main representatives though few and far apart. The lower layer is a dense mat of *Astelia papuana* Skottsberg, species of *Gentiana*, *Gleichenia vulcanica* v. A. v. R., *Oreobolus ambiguus* Kük. and v. St., *O. pumilio* R. Br., *Oreomyrrhis andicola* Hook. f, *Plantago lanigera* Hook. f., *Ranunculus amerophyllus* F. Muell., and several species of *Potentilla*. These plants owing to water movements in the surface, sometimes form mushroom shaped tussocks by the erosive action on the intermediate soil.

7. The *Plantago-Euphrasia-Sphagnum* aspect is a widespread aspect mainly on seepage slopes, but also along creeks, tracks, rivulets, banks of ponds or in wet places with a relatively stagnant surface water. It is a one-layered vegetation of a few species only, with a dominance of several species of *Euphrasia*, *Plantago aundensis* van Royen, *P. depauperata* M. and P., *P. lanigera* Hook. f., *Ranunculus amerophylloides* Eichler, and sometimes a few scattered specimens of *Gentiana ettingshausenii* F. Muell. Large patches of *Sphagnum* are a distinct feature of this aspect, often to the exclusion of any other species.

8. The bogs, ponds, marshes and tarns are treated here as one aspect because their composition is essentially the same, with a reduction in number of species towards the larger sized water surfaces, so that in the larger ponds only *Isoetes sp.*, *Callitriche verna* L, species of *Haloragis* and an occasional grass (*Poa egregia* Chase) is found. The smaller ponds etc., often carry a vegetation that is in no way different from the surrounding wetter slopes.

9. In the alpine areas many creeks and rivulets develop under the moist conditions at these altitudes. Most of these, however, are only temporarily and periodically flooded with water and the vegetation

on their banks differ hardly from the vegetation of any of the previous aspects, though a more luscious development of grasses like *Danthonia archboldii* Hitchc. can be noticed. In general these temporary creeks are shallow and often are mere bogs or swampy. Well developed creeks with permanent water are relatively few in the alpine areas. They often cut out deep and steep gulleys and a vegetation of tree-ferns. *Rhododendrons* and *Vacciniums* and other species of the subalpine shrubberies overhang these gulleys making impenetrable tunnels.

On the open banks dense tufts of grasses such as *Deschampsia klossii* Ridley, *Danthonia archboldii* Hitchc., are interspersed with low cushions of *Cerastium papuanum* Mattf., *Galium australe* DC, *Plantago depauperata* M. and P., *P. lanigera* Hook. f, *Ranunculus amerophyllus* F. Muell., *Trigonotis robusta* Johnston, while more rare are species of *Euphrasia*, *Lagenophora stipitata* Labill., *Lobelia angulata* Forster, *L. conferta* M. and P. and the strikingly beautiful *Epilobium* and *Viola* species. Occasionally the forget-me-nots (*Myosotis saruwagedica* Schlechter) form large clumps but in general this is a rare species. In the creeks large patches of *Scirpus fluitans* Hook. f. and *Callitriche verna* L, wave to and fro in the rapid running water.

At the higher altitudes near the summit the vegetation of the creekbanks approaches that of the surrounding areas and in that respect resemble the vegetation of the temporary creeks mentioned.

10. The seepage slopes can be regarded as one of the few places from where some of the elements of the alpine vegetation originated. They are usually found on slopes, though the latter are sometimes so slight as almost to be imperceptible. In all cases studied these seepage slopes had an impermeable layer of a pale brownish sandy clay at depths varying from a few centimeters to about one meter. In the former case the water is more a surface layer than true seepage. For the composition of its vegetation cover this seemingly makes no difference.

The vegetation is rather dense and essentially a one-layered one, though with deeper clay-layers it will become richer and approaches that of the wet grasslands with its various vegetations. It must be pointed out here that as everywhere in the grasslands usually no sharp distinction exists between the different aspects, and that only a sharp change in soil composition is followed by a distinct change in vegetation.

The main components of the vegetation of the seepage slopes are small grasses and low herbs as *Centrolepis philippinensis* Merrill, *Euphrasia sp.*, *Gentiana cinereifolia* van Royen, *G. ettingshausenii* F. Muell., *Oreobolus spp.*, *Ranunculus amerophyllus* F. Muell., *R. amerophylloides* Eichler, *Plantago aundensis* van Royen, *P. depauperata* M. and P., *P. lanigera* Hook. f., *Tetramolopium alinae* (F. Muell.) Mattf., and *T. ciliatum* Mattf.

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CYTOTAXONOMIC NOTES ON SOME GALIUM SPECIES

E. KLIPHUIS

(*Botanical Museum and Herbarium, Utrecht*)

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It is well known that the chromosome number of a plant may be a character of importance to taxonomy; it can often give a better insight with respect to the place of a taxon in the System. It is, therefore, particularly important to determine for any species the chromosome number of as many individuals from as many localities as possible. Publications of lists of documented chromosome numbers as presented by Löve in the IOPB reports in Taxon are very valuable and so are lists of chromosome numbers of plants from more restricted areas (Greenland: Jörgensen *et al.*, 1958; Iceland: Löve and Löve, 1956; the Netherlands: Gadella and Kliphuis, 1963; Poland: Skalinska, 1950, Skalinska *et al.*, 1957, 1959, 1961; Sweden, Skåne: Lövkvist, 1962).

These lists enable us to ascertain whether or not there are differences in chromosome numbers within a species and whether or not there is a relation with the geographical distribution or the ecological preference. Apart from the number, however, the size and shape of the chromosomes and, consequently, their 'portrait' may be of value. In the *Angiospermae* this character plays an important role almost exclusively in the *Monocotyledones*.

Differences in chromosome number within a species or species complex are sometimes, but certainly not always correlated with differences in morphology (*Viola riviniana* with $2n = 35$, 40, 45, 46 and 47, Gadella, 1963; *Listera ovata* with $2n = 34$, 35, 36 and 38, Kliphuis, 1963). Even on the level of polyploidy (*Galium verum* with $2n = 22$ and 44, Lövkvist, 1962), we encounter this situation. The reverse situation also occurs: the species *Galium mollugo* L., collected in 91 different localities, always appeared to be a tetraploid ($2n = 44$) but even though showing a great morphological variability which remains constant after several years of cultivation.

A careful analysis of the chromosome number of *Galium aparine* L., a species having a polyploid series with $2n = 22$, 44, 66 and, according to Fagerlind (1934), $2n = 88$, clearly showed that the level of polyploidy rather than the exact number of chromosomes is important.

The hexaploids generally have $2n = 64$, but within the same plant metaphase plates from the same roottip may have $2n = 61$, 62, 63, 65 and the normal hexaploid number $2n = 66$. However, we also found plants with 66 chromosomes in all countable metaphase plates of the same roottip.

The same phenomenon has been found in *Cardamine pratensis* L. (BERG, 1966), and in *Symphytum officinale* L. (GADELLA and KLIPHUIS, in press).

Before arriving at a final conclusion it may be necessary to investigate other characters besides the chromosome number. The *Dactylorchis maculata* complex has been shown to have a diploid with $2n = 40$ as well as a tetraploid with $2n = 80$ chromosomes. VERMEULEN (1947) separated the diploid from the tetraploid and described it as *Dactylorchis fuchsii* (Druce) Vermln. Not only on account of those numbers but also because of morphological and ecological differences. Extensive biometric work by HESLOP-HARRISON (1948, 1951, 1954) on a considerable amount of material confirmed this conclusion.

Plants belonging to the *Dactylorchis maculata* complex occuring in the Netherlands were cultivated under identical conditions for several years. It was shown that differences between the diploid *Dactylorchis fuchsii* and the tetraploid *Dactylorchis maculata* became less clear, already after one year (KLIPHUIS, 1963).

From these examples it is clearly necessary to make cultivation experiments before expressing oneself definitely on such problems.

Galium hercynicum Weig. provides an example of a species in which morphological differences are correlated with the level of polyploidy. These differences remained constant during several years of cultivation. The diploid ($2n = 22$) is distinguished from the tetraploid ($2n = 44$) by a more fragile habit, more slender shoots, smaller flowers and leaves, and by the fact that it flowers about two weeks earlier than the tetraploid. *Galium hercynicum* is a common plant of Western Europe (southern Scandinavia, Denmark, Germany, Belgium, the Netherlands, France, northern Spain, Portugal and the British Isles).

The results of the measurements of the flowers are given in Table 1. In the first column: the investigated plants with the collection

TABLE 1

(Measurements of the flowers)

Flower 1963 in mm		*X*	*SD*	*SE*	*N*
No. plant; diploid $2n = 22$					
106	*L*	2.881	0.2047	0.0206	99
	W	0.811	0.1082	0.0108	100
244	*L*	3.038	0.2565	0.0257	100
	W	0.931	0.0896	0.0090	100
tetraploid $2n = 44$					
386	*L*	3.898	0.2224	0.0222	100
	W	0.953	0.1132	0.0113	100
414	*L*	3.992	0.1212	0.0121	100
	W	1.021	0.0608	0.0061	100

Leaf 1963 in mm			I				II				III				IV			
			X	*SD*	*SE*	*N*	*X*	*SD*	*SE*	*N*	*X*	*SD*	*SE*	*N*	*X*	*SD*	*SE*	*N*
106 diploid $2n = 22$	1962	*L*	3.332	0.655	0.12	30	3.552	0.747	0.144	27	1.350	0.698	0.174	16	3.640	0.408	0.091	20
		W	0.582	0.265	0.045	33	1.028	0.131	0.025	27	0.690	0.397	0.099	16	1.288	0.222	0.049	20
	1963	*L*	4.432	0.800	0.080	100	4.200	0.498	0.050	100	2.656	0.635	0.090	50	4.112	0.824	0.117	50
		W	0.681	0.175	0.017	100	0.975	0.154	0.015	100	0.933	0.069	0.021	50	1.312	0.219	0.031	50
	1964	*L*	4.728	0.614	0.061	100	4.560	0.828	0.117	50	2.976	0.584	0.082	50	4.256	0.947	0.134	50
		W	0.763	0.118	0.012	100	1.173	0.270	0.038	50	1.085	0.295	0.042	50	1.291	0.178	0.025	50
244 diploid $2n = 22$	1962	*L*	4.713	1.016	0.126	64	4.880	1.286	0.181	50	2.984	0.723	0.218	11	4.512	1.272	0.127	100
		W	0.764	0.302	0.039	60	1.139	0.258	0.036	50	—	—	—	—	1.564	0.204	0.022	90
	1963	*L*	4.248	1.024	0.102	100	4.288	1.096	0.122	80	2.664	0.817	0.122	45	4.224	0.592	0.070	71
		W	0.641	0.265	0.027	95	0.964	0.270	0.031	75	0.788	0.293	0.046	40	1.626	0.271	0.033	66
	1964	*L*	4.336	0.896	0.090	100	4.328	1.109	0.111	100	2.720	0.775	0.110	50	4.272	0.712	0.071	100
		W	0.752	0.257	0.026	100	0.976	0.206	0.021	100	0.837	0.189	0.027	50	1.704	0.274	0.027	100
386 tetraploid $2n = 44$	1962	*L*	5.912	1.144	0.114	100	6.880	1.688	0.169	100	4.526	1.016	0.110	70	5.312	1.066	0.107	100
		W	0.841	0.324	0.032	100	1.448	0.191	0.019	100	1.520	0.372	0.044	70	2.326	0.284	0.028	100
	1963	*L*	6.120	1.208	0.121	100	6.792	1.144	0.114	100	3.560	0.673	0.067	100	5.768	1.472	0.147	100
		W	0.830	0.317	0.032	100	1.483	0.197	0.020	100	1.517	0.272	0.027	100	2.205	0.257	0.026	100
	1964	*L*	6.064	1.392	0.139	100	7.864	1.568	0.157	100	4.680	0.801	0.127	40	5.328	1.546	0.218	50
		W	0.839	0.084	0.008	100	1.636	0.215	0.022	100	1.582	0.233	0.039	40	2.059	0.256	0.026	100
414 tetraploid $2n = 44$	1962	*L*	5.128	0.917	0.092	100	7.072	1.046	0.105	100	3.400	0.869	0.087	100	4.480	1.212	0.169	50
		W	0.937	0.179	0.018	100	1.754	0.202	0.020	100	1.478	0.226	0.032	50	1.822	0.299	0.042	50
	1963	*L*	5.680	1.488	0.016	90	6.720	1.480	0.171	75	3.264	0.422	0.060	50	5.424	1.216	0.122	100
		W	0.993	0.297	0.031	90	1.734	0.493	0.057	75	1.654	0.349	0.049	50	2.435	0.322	0.032	100
	1964	*L*	5.736	1.167	0.118	100	7.128	1.168	0.117	100	3.656	0.730	0.073	100	5.200	0.960	0.096	100
		W	1.069	0.362	0.036	100	2.271	0.346	0.035	100	1.420	0.289	0.029	100	2.300	0.246	0.025	100

numbers, (the diploids: 106 and 244; the tetraploids: 386 and 414; localities: 106: Portugal, Botanical Garden Sacavem, 244: Portugal, Tras os Montes, Lisa do Alvoa; 386: the Netherlands, Zuid-Limburg, 414: the Netherlands, Duurswoude, prov. of Friesland). In the following columns is L = length, W = width both in mm, X = the mean of the length or width of the sample, SD the standard deviation, SE the standard error of the mean and N = the total number of the sample.

It is clear that there is a difference in length of the flowers between the diploid and tetraploid. Most striking, however, is the difference in size of the leaves. Three types of leaves can be distinguished on the flowering shoots: Type I, leaves on the upper third part of the shoot; Type II, those of the middle third part of the shoot, and Type III, the smallest leaves on the lowest part, mostly wilted. A fourth type is found on the non-flowering shoots.

The measurements of the leaves are given in Table 2. From these tables the differences between the diploid and tetraploid are evident. The same is true for the differences between the leave types mentioned before. It is also clear from the values given that these differences remain constant over the years.

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ON THE WATER RELATION IN LIMESTONE AND DIABASE VEGETATION IN THE LEEWARD ISLANDS OF THE NETHERLANDS ANTILLES

A. L. STOFFERS and C. J. A. MANSOUR ELASSAISS

(*Botanical Laboratory of the University, Nijmegen*)

(*received November 19th, 1965*)

Abstract

In a same macroclimate on the islands of the Leeward Group of the Netherlands Antilles two types of vegetation are chiefly found. A vegetation pertaining to the dry evergreen formation series on limestone and a vegetation on diabase belonging to the seasonal formation series. Study was made of the water relation at the end of the rainy season during which transpiration, water deficit, suction pressure and soil water were investigated. From the course of transpiration curves it was concluded that water relations in diabase soil are more sever than those in the limestone. Water deficit in plants, growing on diabase appears to be much higher than those of limestone. Suction pressure divergates strongly in both cases. In the upper soil layers the amount of water that can be taken up by plants is small both in limestone and diabase. In deeper layers of the limestone soil there is more water than in diabase of the same level. Vegetation on diabase is determined by a sufficient amount of water in the soil during the rain season and a great drought during the other months. On the other hand in limestone the amount of water in the soil is larger during a longer period. Because of the higher suction pressure of this soil only plants developing a higher suction pressure can occur.

1. Introduction

The vegetation of the Leeward Islands of the Netherlands Antilles, situated at a distance of 27 to 87 km from the Venezuelan coast, is determined by the tropical temperatures, but more so by the great drought which exists here during several months of the year (Boldingh, 1914; Stoffers, 1956). An exception must be made for vegetation types such as mangrove woodlands, vegetations of saltflats and salinas, and fresh and brackish water communities. These types are indicated by Beard (1944, 1949) as 'Edaphic climax Formations and derivates'.

Boldingh (1914) distinguishes besides these vegetations – indicated by him as littoral vegetations – a Croton vegetation '. . . determined by *Acacia* and *Croton*, which has either a *Capparis* or a *Rhacoma* type, to be found on diabase and limestone respectively. In the higher parts of the island this *Croton* vegetation changes into a more forest-like type'. Stoffers (1956) distinguishes besides the edaphic communities a seasonal formation series on diabase and a dry evergreen formation series, mainly on the quaternary limestone. The distinction in the two mentioned series was based on the classification of vegetation types of tropical America put foreward by Beard (1944, 1949).

These seasonal and dry evergreen series differ not only in composition of the species, but especially in structure. BEARD (1949) assumes that the seasonal formations as a rule are 'an expression of physical drought and consequently deciduous trees are typical, rather than hard-leaved evergreens. Under the driest conditions thorniness and microphylly become characteristic. On the other hand, dry evergreen formations occur in relatively dry areas, but they are the expression of physiological rather than physical drought'. The species typical for these formations are hard-leaved evergreens; under drier conditions microphylly is characteristic, but not thorniness.

In spite of strong anthropogenic influences there is a marked difference between the vegetation of the limestone plateaux and that of the non-calcareous areas in the islands of Aruba, Bonaire, and Curaçao. Therefore, these islands seem to be very suitable for an ecological investigation as here limestone and diabase are found side by side in the same macroclimate. Meteorological observations do not indicate that there are differences in amounts of precipitation between limestone and diabase areas, through which the difference in vegetation could be explained.

Seeing the great correlation of seasonal formations and derivates with diabase on the one side and dry evergreen formations and derivates with limestone on the other side, one could decide to a calcifuge and a calcicole vegetation. Species that could be taken into consideration as calcicole are among others *Antirrhoea acutata*, *Bulbostylis curassavica*, *Rhacoma crossopetalum*, and *Erithalis fruticosa*. This is definitely not the case with species such as *Coccoloba swartzii*, *Bumelia obovata*, and *Metopium brownei*, species that are particularly characteristic of the limestone area and often determine the physiognomic aspect. However, they also occur on the slope of the Seroe Christoffel in Curaçao, on the steep slopes of the Brandaris and the Joewa Hills in Bonaire (STOFFERS, 1963), and on the Arikok in Aruba. BEARD (1949) has also reported similar observations.

The purpose of this investigation was to gain an insight into the ecological differences between these vegetation series.

From an ecological point of view five primary factors must be discerned (WALTER, 1960): 1. heat, 2. water, 3. light, 4. chemical, and 5. mechanical. This investigation was deliberately limited to heat and water factor. The other primary factors were not studied since there is no reason to suppose that great differences in light or sharp variations in mechanical damage occur on limestone and diabase. This, of course, is not the case with the chemical factor. Distribution of a number of species mentioned earlier indicates that the influence of calcium is probably not a primary one. It possibly influences the water relation of the soil, where it plays an important role in the development of the clay complex.

Results concerning the heat factor, especially the differences in micro-meteorological circumstances will be published elsewhere.

Since the water factor affects both in the atmosphere and in the soil, an effort was made to obtain data not only on transpiration, suction pressure of the leaves, and the water saturation deficit, but also on the water content of the soil. It must be emphasized that for some measurements it was not the intention to gather absolute but rather relative values e.g. for soil humidity and saturation deficit.

2. METHODS

Under field conditions one is strongly limited in the applied methods as it demands portable instruments. We had devised the following methods for our use:

Transpiration. It was determined by the Momentan-method (STOCKER, 1929; STEUBING, 1965). The loss of water per minute, per gramme of the leaf was measured. Leaves not older than one year and of the same exposition were used. These were weighed on the spot immediately after being removed from the plant and were freely exposed for two minutes and weighed again. A torsion balance (Verenigde Draadfabrieken, Nijmegen, The Netherlands) was used for these measurements.

Evaporation. It was measured with the aid of a PICHE evaporimeter.

Suction pressure of the leaf. This was determined by the method of SCHARDAKOW, a method which had already proved to be very useful (SCHARDAKOW, 1956; MOURAVIEFF, 1959; REHDER, 1959, 1960, 1961; REHDER and KREEB, 1961; STEUBING and WILMANNS, 1962; STEUBING, 1965). In this method, pieces of leaves are placed in a series of saccharose solutions of decreasing concentrations. After 90 min. this test solution is coloured with methylene-bluc and a drop is introduced into the corresponding initial concentration. The suction pressure is found at the value at which the drop remains afloat. This method was used since relative values rather than absolute values were sought.

Water saturation deficit. For the saturation deficit, a method developed by ČATSKÝ was used in which punched-out pieces of leaves measuring about 1½ cm in diameter were employed instead of branchlets (ČATSKÝ, 1960; STEUBING, 1965). Saturation takes place in a foam-plastic plate. The saturation deficit is given in percentages of the saturation weight and is calculated according to the formule

$$S_{\mathrm{rel}} = \frac{W_{\mathrm{max}} - W_{\mathrm{i}}}{W_{\mathrm{max}}} \times 100,$$

in which S_{rel} is saturation deficit, W_{i} the initial weight and W_{max} the weight of the pieces at saturation.

Water content of the soil was determined by a somewhat modified plasterblock method after BOUYOUCOS and MICK (1940). In this method electrodes made of small-mesh wire-netting are separated from each other by a 3 mm broad plastic ring (KÖHN and PERSON, 1950). Then to both sides of these electrodes plastic rings also 3 mm broad, are applied and the entire structure is filled with plaster of Paris (Néo-Mouledur, Poliet and Chausson, Paris). The electrical resistance between the electrodes in the plaster blocks was used as an indication for the soil humidity. This electrical resistance was measured with the aid of a Wheatstone bridge.

3. VEGETATION

The areas of investigation lie scattered across the island of Curaçao. The measurements mentioned here were taken at five sites with a vegetation like that which is characterised here:

3.1. *Malpais*

A *Croton* thicket on diabase, which is only slightly or not at all under the influence of the trade-wind, with some scattered trees. Outside the plot some specimens of *Balanites aegyptica* were found, a tree that was introduced in 1880 and since then has spread over the eastern part of the island. Vegetation covers 65 % of the surface and reaches a height of 70 cm. Composition of the vegetation is given here after the Braun-Blanquet scale (BRAUN-BLANQUET, 1951; KNAPP, 1958). *Croton flavens* 3.2; *Acacia tortuosa* + 0.1; *Opuntia wentiana* + 0.1; *Acacia curassavica* 1.2; *Heliotropium ternatum* 1.2; *Haematoxylon brasiletto* r; *Aristida adscencionis* 1.2; *Bouteloua heterostega* + 0.1; *Euphorbia thymifolia* + 0.1; *Anthephora hermaphroditica* + 0.2.

3.2. *Hill near Janwé*

A diabase hill with a *Croton* vegetation in which some scattered trees occur. This site is highly exposed to influences of the wind. Vegetation height amounts 50–60 cm and cover about 40 %. *Croton flavens* 3.2; *Lantana camara* + 0.1; *Opuntia wentiana* + 0.1; *Bourreria succulenta* r; *Haematoxylon brasiletto* + 0.1; *Caesalpinia coriaria* + 0.1; *Pectis humifusa* + 0.1; *Anthephora hermaphroditica* + 0.2; *Euphorbia thymifolia* + 0.1. Outside of the plot some specimens of *Bursera bonairensis* were found.

3.3. *Noordkant Plantation*

The soil occupies pockets and crevices in a general expance of hard limestone pavement. Vegetation height is 2–3 m and this is overtopped by some scattered higher trees. It is classified as dry evergreen woodland, and is considered to be one of the best vegetated limestone plateaux of the islands. *Coccoloba swartzii* 3.2.; *Rhacoma crossopetalum* 1.2; *Caesalpinia coriaria* r; *Bourreria succulenta* r; *Haematoxylon brasiletto* + 0.1; *Metopium brownei* 2.2; *Antirrhoea acutata* 2.2; *Cordia cylindrostachya* + 0.1; *Casearia tremula* + 0.1; *Lantana camara* + 0.1; *Opuntia wentiana* r; *Cephalocereus lanuginosus* v.r.; *Croton flavens* + 0.1.

3.4. *Siberie*

A limestone plateau in the middle of the island with a rather dense vegetation comparable with the former. *Coccoloba swartzii* 3.1;

Haematoxylon brasiletto 1.1; *Metopium brownei* + 0.1; *Bumelia obovata* r; *Randia aculeata* + 0.2; *Bourreria succulenta* 1.1; *Acacia tortuosa* r; *Croton flavens* r; *Antirrhoea acutata* 2.2; *Lantana camara* + 0.1; *Phyllanthus botryanthus* + 0.1; *Erithalis fruticosa* + 0.1; *Cordia cylindrostachya* + 0.1.

3.5. *Mahoema*

A limestone plateau near the north coast of the island. The vegetation is considered to belong to the '*Croton-Lantana-Cordia* thicket derived from dry evergreen woodland' (STOFFERS, 1956). The vegetation in which Antirrhoea acutata and Erithalis fruticosa dominate is in general less than 1 meter high and a few scattered higher shrubs or small trees occur. *Antirrhoea acutata* 2.2; *Erithalis fruticosa* 2.1; *Cordia cylindrostachya* 1.1; *Croton flavens* + 0.1; *Lantana camara* + 0.1; *Opuntia wentiana* + 0.1; *Casearia tremula* r; *Haematoxylon brasiletto* r; *Cyperus planifolius* + 0.2.

4. OBSERVATIONS

4.1. *Transpiration*

Figures 1 and 2 show an example of transpiration in plants on diabase obtained at Janwé and Malpais. It is evident that in both cases transpiration reaches a maximum value in the morning hrs. This is followed by a sharp fall. The time at which the maximum is reached differs from species to species and the place where the plant grows. At Janwé, *Croton flavens* and *Bourreria succulenta* have a maximum in the early morning hours while for *Bursera*, *Haematoxylon*, and *Caesalpinia coriaria* this maximum is shifted to a time more close to noon. Both of these types occur also in Malpais. *Acacia tortuosa*, *Acacia curassavica*, and *Phyllanthus botryanthus* have their maximum in the morning hours. For *Balanites* and *Croton* the maximum is shifted to an earlier hour in the case of Janwé. This phenomenon could be explained on the basis of the trade wind as on sites strongly exposed to this wind a shift of the maxima to an earlier hour is always observed for the species. In the case of *Caesalpinia* and the non-native *Balanites* a maximum is found considerably higher in comparison with the other species while a conspicuously lower transpiration maximum is found in *Phyllanthus botryanthus*. The course of transpiration in the mentioned species is thus represented by a 'one-topped' curve in which the maximum is found in the early morning hours or about noon.

A different type of curves is seen in Fig. 3, 4, and 5. Here the majority of the species show two maxima in the Course of the day, a 'two-topped curve'. The first top is found in the early morning hours and the second one in the afternoon and these are separated by a minimum at about noon. As can be seen in Fig. 3 it is evident that *Antirrhoea*, *Erithalis*, and *Phyllanthus* can decrease transpiration to a value that could not be measured by the applied method. *Antirrhoea* has a strong xeromorphic structure with heavily cutinised shiny leaves. *Erithalis* has more or less succulent leaves with a thick

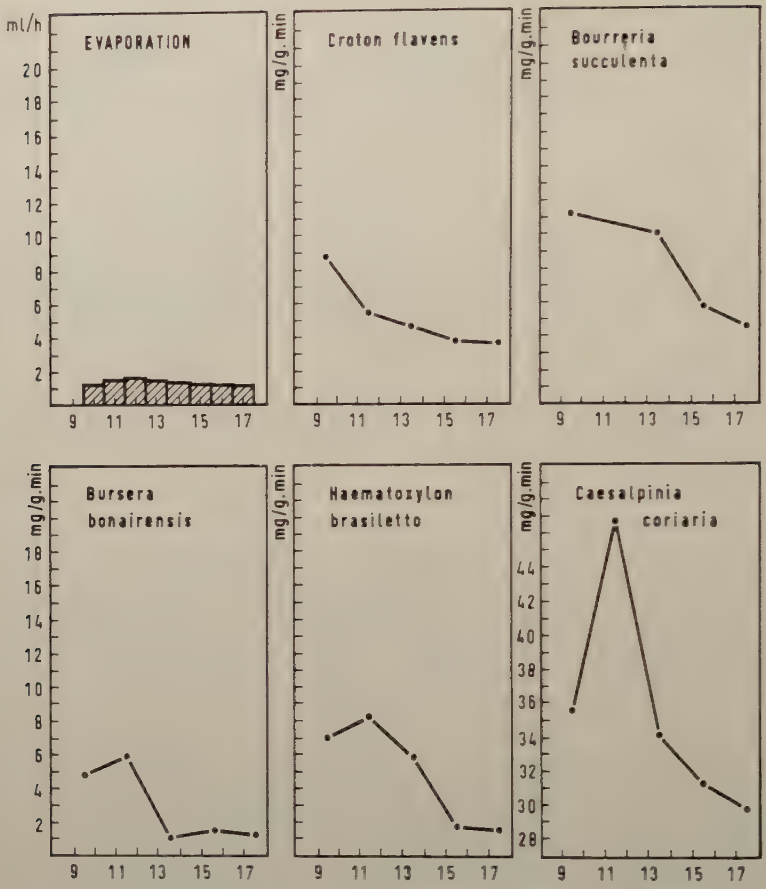

Fig. 1. Evaporation and transpiration. Janwé, 14–2–1964.

cuticle, while *Phyllanthus* can curl the leaves to decrease transpiration. *Metopium* is conspicuous in this group by its high maximum values which, however, were not found in other locations. Among the most striking species are *Croton flavens* and *Haematoxylon brasiletto* where completely different types of curves are seen. In *Croton* corresponding with the evaporation curve, a slow increase is noticed during the morning hours and a gradual decrease in the afternoon. *Haematoxylon* represents the 'one-topped' curve with a maximum strongly shifted to the morning hours. The same is seen in Fig. 4. The majority of species show a 'two-topped' curve with a minimal transpiration about noon time. *Croton* here again forms an exception with a gradually increasing transpiration more or less proportional to the evaporation. However, there is a strong decrease in the course as the afternoon approaches.

In the third example of a vegetation on limestone, Fig. 5, where the low shrubs determine the aspect, the two-topped curves occur

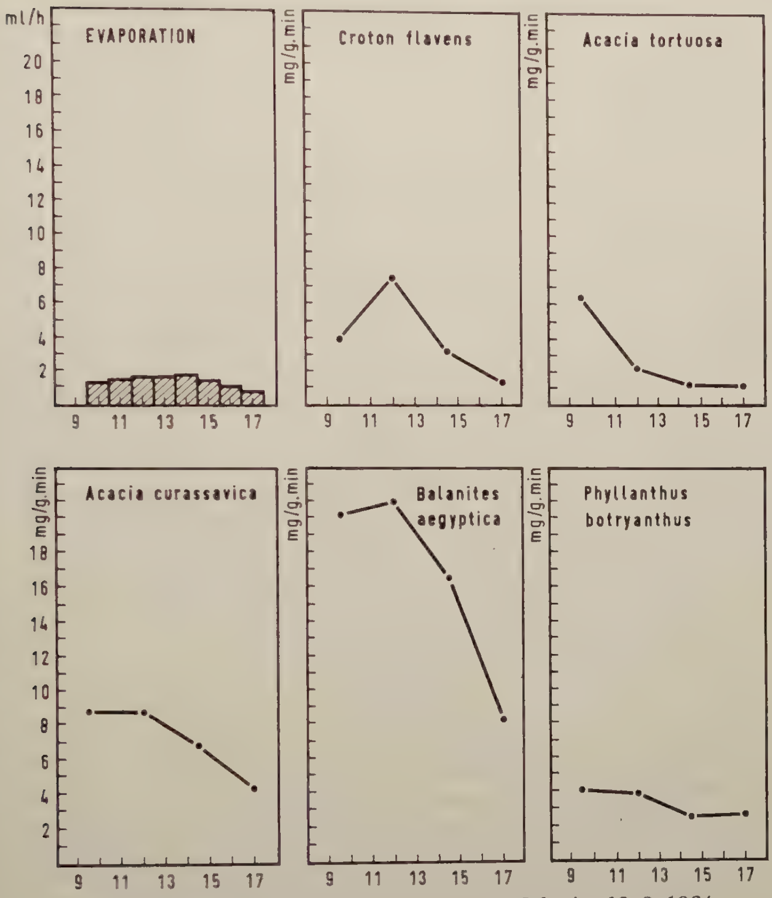

Fig. 2. Evaporation and transpiration. Malpais, 12–2–1964.

in four of the five species. Here again an exception is seen in *Croton flavens* which shows a curve parallel to evaporation. It is evident from the examples given, that three types of transpiration can be discerned viz.:

1. a two-topped curve in which the minimum is reached about noon-time indicating a strong decrease in transpiration;
2. a one-topped curve in which the maximum is shifted to the early hours of the day;
3. a symmetrical curve which runs more or less parallel to the evaporation curve.

4.2. *Water saturation deficit*

The saturation deficit will increase faster and to a higher value depending upon the lower resistance to periods of drought by the

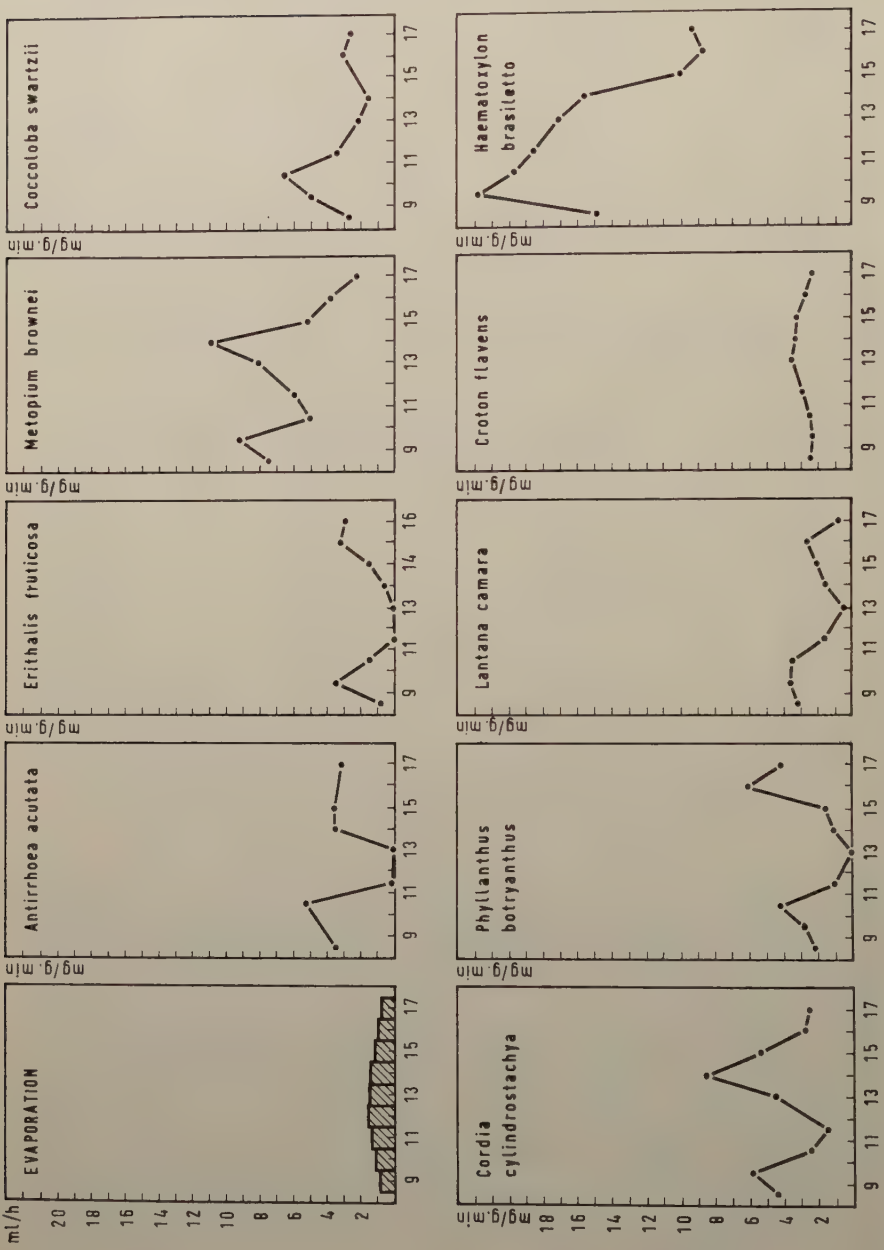

Fig. 3. Evaporation and transpiration. Siberie, 7–2–1964.

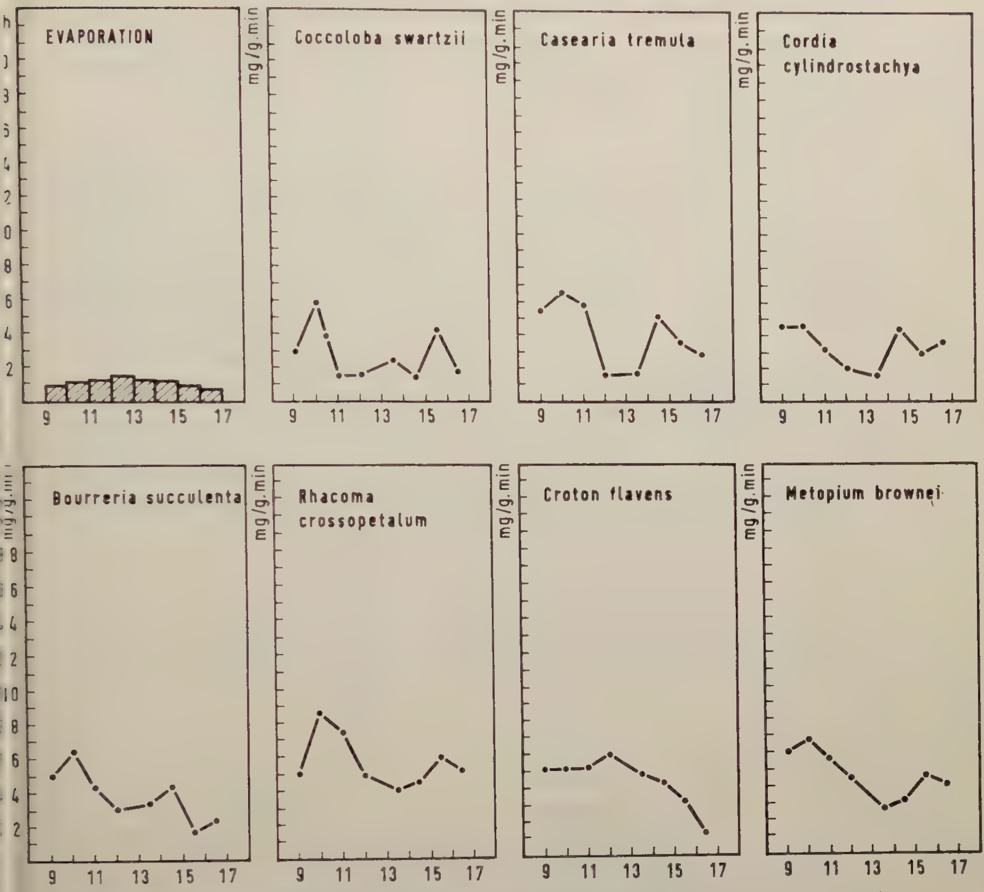

Fig. 4. Evaporation and transpiration. Noordkant Plantation, 27–1–1964.

plant. In general this is the case with species which have higher demands on the water household. Table I confirms the conclusions drawn from the course of the transpiration.

It is evident that on days of observation at the end of the rainy season a difference becomes apparent between plants which grow on limestone and those which grow on diabase. In the species on the limestone plateaux there is a maximal saturation deficit in the order of 10% at this time of the year. This maximum value seems to be a minimum in the plants on diabase, the maximum in these plants being 30%. These differences are well brought out in the cases where the saturation deficit was measured in plants that occur both on limestone and on diabase namely *Croton flavens*, *Bourreria succulenta*, *Haematoxylon brasiletto*, and *Phyllanthus botryanthus*.

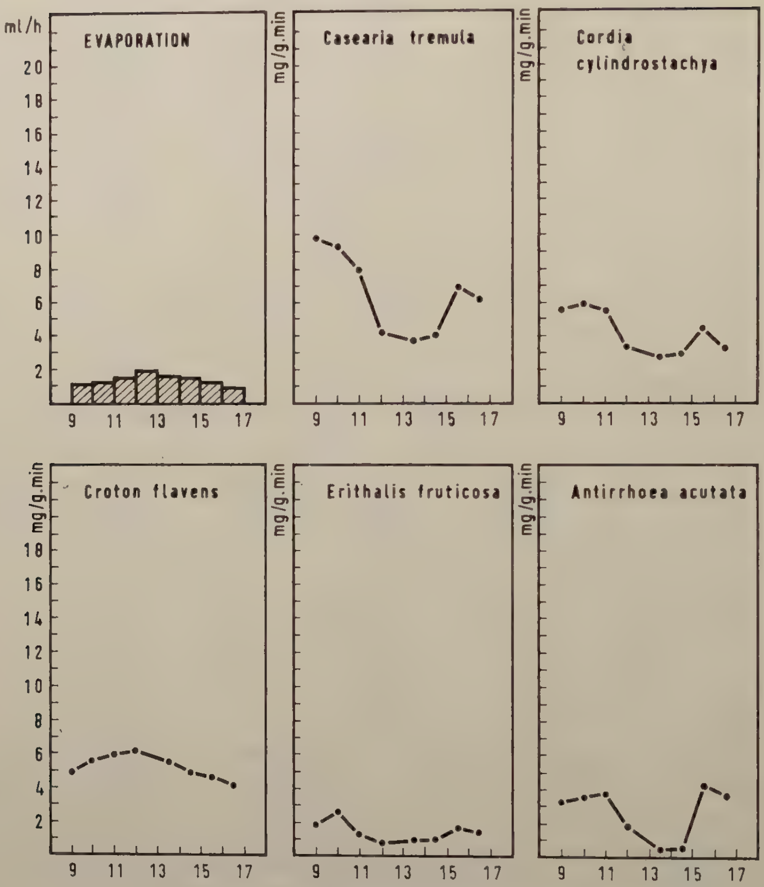

Fig. 5. Evaporation and transpiration. Mahoema, 23–1–1964.

4.3. *Suction pressure*

The observation that transpiration-decrease can be the result of lower suction pressure, a better insight in the water relation can be obtained through informations gained from the measurements of the suction pressure.

In contrast to the osmotic values which can be regulated within certain limits in relation to the location, the suction pressure is a more variable unit which is determined by the interplay of the osmotic and the turgor pressure (Meyer, 1956). The suction pressure is not very much dependent on general average circumstances, but on momentary meteorological and soil water conditions. As a result of this, the suction pressure often shows considerable daily fluctuations. In Table 2 the suction pressure of a number of plants is shown along with their locations. Some of the measurements which the present authors for some purpose consider not reliable altogether are indicated by x.

TABLE 1

Water saturation deficit in plants growing on diabase and limestone

	Janwé	Malpais	Siberie	Noord kant	Mahoema
Bursera bonairense	13 %				
Bourreria succulenta . . .	27 %				
Haematoxylon brasiletto .	24 %		10 %		
Croton flavens	28 %	17 %	6 %	7 %	9 %
Acacia curassavica		10 %			
Balanites aegyptica		30 %			
Phyllanthus botryanthus .		21 %	5 %		
Coccoloba swartzii			9 %	7 %	
Cordia cylindrostachya . .			5 %	6 %	7 %
Metopium brownei			4 %	10 %	7 %
Erithalis fruticosa			11 %		10 %
Antirrhoea acutata			3 %		10 %
Lantana camara			8 %		
Rhacoma crossopetalum. .				4 %	
Casearia tremula				6 %	8 %

TABLE 2

Suction pressure of some plants growing on diabase and limestone

abase	9.30	13.00	17.00 h.		9.30	13.00	17.00 h.
nwé				Malpais			
esalpinia coriaria	10	31	23	*Acacia curassavica*	10	32	27
rsera bonairensis	3.5	18	21	*Croton flavens*	13	34	25
ematoxylon brasiletto	21	45	x	*Acacia tortuosa*	13	27	24
ton flavens	12	32	24	*Randia aculeata*	19	29	29
urreria succulenta	8	30	26	*Phyllanthus botryanthus*	16	33	27
mestone							
oordkant Plantation				Near Willemstad			
ccoloba swartzii	6	13	19	*Croton flavens*	9	16	13
tirrhoea acutata	6	10	10	*Cordia cylindrostachya*	x	8	10
acoma crossopetalum	4	15	13	*Acacia curassavica*	x	4	6
urreria succulenta	13	21	19	*Acacia tortuosa*	x	8.5	5
rdia cylindrostachya	8.5	22	20				
ear Piscadera				Siberie			
urreria succulenta	8.5	26	18	*Bumelia obovata*	19	18	x
searia tremula	9	25	14	*Rhacoma crossopetalum*	18	22	18
aematoxylon brasiletto	20	22	15	*Randia aculeata*	26	26	21
esalpinia coriaria	20	20	22				
osopis juliflora	15	11	11.5				
cacia tortuosa	16	18	15				

4.4. *Water content of the soil*

A frequent and regular measuring of the water content of the soil was impossible. Firstly these locations are situated too far from each other and secondly, the stay in Curaçao was interrupted by a trip to the island of Bonaire. However, a good impression is given by the data collected near Janwé and at Noordkant Plantation. These measurements were made on the same day at 5 and 25 cm depths at 5 days intervals during the end of the rainy season. The electrical resistance (in Ohms) between the electrodes in the plasterblocks is given in Fig. 6.

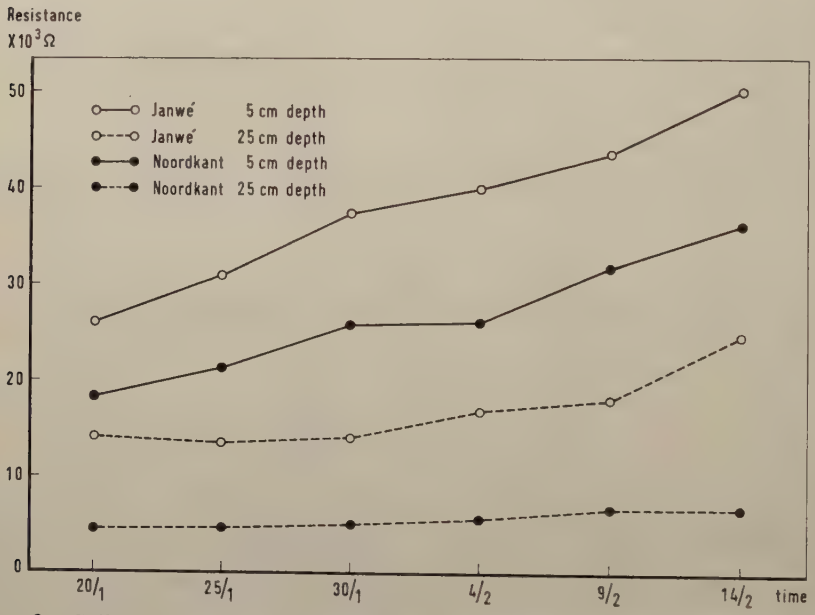

Fig. 6. Soil moisture; data obtained by the modified Bouyoucos-method. Resistance given in Ohms.

These data are mean values of three measurings. From the data it is clear that at this time of the year the limestone soil below 25 cm depth is moister than the diabase soil. Differences are smaller at 5 cm depth. It must be emphasized that water relations may shift strongly in the course of the year, as is shown by data collected in the island of Bonaire during the rainy season.

5. DISCUSSION

If the data presented here are overlooked, then a marked difference in the water relation between plants growing on diabase and limestone becomes evident. In the first place this difference is seen in transpiration. The three types in the transpiration curves seen, reflect

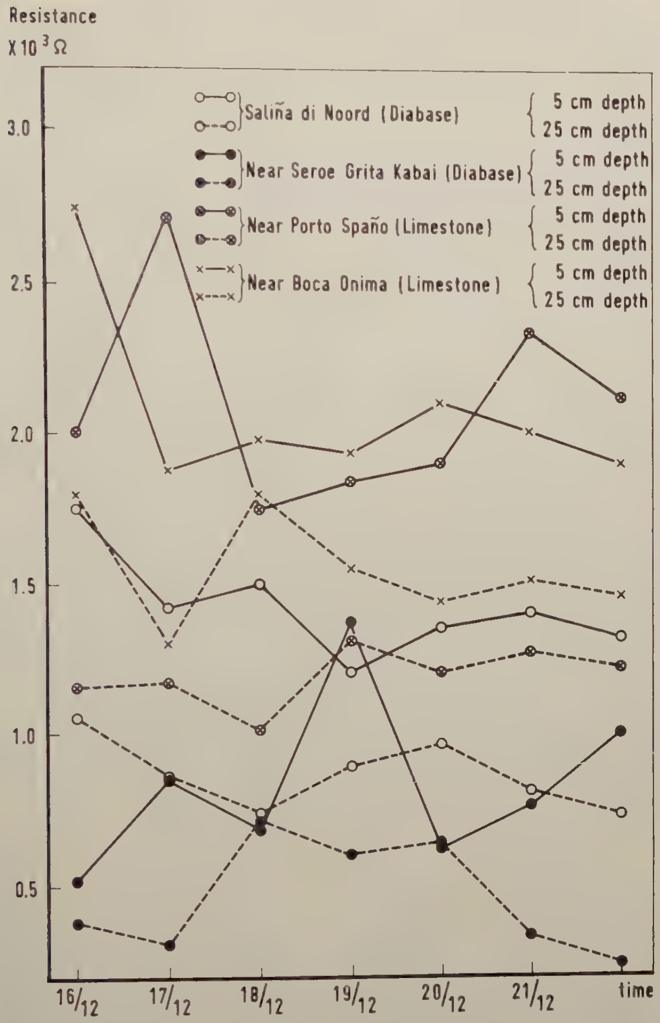

Fig. 7. Soil moisture data obtained in the island of Bonaire. Resistance given in Ohms.

clearly the water relation in the soil. If the amount of soil water is adequate the transpiration curve runs parallel to the evaporation curve (STOCKER, 1956). This is the case with *Croton flavens* growing on limestone. If this species occurs on diabase then the rate of transpiration decreases after reaching the maximum disproportionate to the decrease in evaporation. This implies that in the soil, the water supply is impeded and the water relation becomes more severe. However it is remarkable that for *Croton flavens* growing on diabase the transpiration maximum is higher than that on limestone. This could be explained either by a capability of *Croton* to develop and stand a high suction pressure in the cell or by a low suction pressure of the diabase soil.

The second type found on diabase can be discerned as the 'one-topped curve' ('Eingipflige Kurve', STOCKER, 1956) in which the maximum is found in the earlier hours of the day. This is brought about due to decrease in transpiration which, however, does not cause a recovery in the hydrature. Therefore, under less unfavourable circumstances in the late afternoon an increase or recovery of the transpiration fails. Due to the occurrence of the one-topped curve in diabase areas it can be concluded that in this time of the year water supply in the soil is not adequate.

In contrast to this, the 'two-topped curve' ('Zweigipflige Kurve') is characterised by the presence of two maxima: one in the morning and one in the afternoon. According to STOCKER (1956) this type is found when there is a more severe water supply in those plants which already limit the transpiration by closing the stomata at a slight loss of water. The decreasing of transpiration will better the water relation and in the course of the afternoon the stomata are reopened and transpiration increases again. This type of transpiration was indicated by BERGER-LANDEFELDT (1936) as iso-hydric. While this type is not found on diabase at all, it is found in the majority of cases on limestone. An exception is seen in *Croton flavens* and in *Haematoxylon brasiletto*. In the former transpiration is proportionate to evaporation. In the latter a one-topped curve is seen and moreover, the difference in transpiration found on the two locations given is very large: 8 mg/gr. min on diabase (Janwé) and 22 mg/gr. min on limestone (Siberie). As can be seen that under given circumstances the evaporation on the site near Janwé is more than near Siberie this difference in transpiration may be explained by a smaller amount of water at the disposal of the plant in the diabase soil.

From the transpirational relations as found at the end of the rainy season it is evident that at this time of the year the hydrative circumstances in the limestone area are more favourable than that in the diabase soil. This conclusion is also supported by the difference in water deficit that is found in plants on diabase-soil and those which grow on limestone. In the latter case values are found that do not surmount 10–11 %. These figures are found at a minimum on diabase.

The low saturation deficit found in plants on limestone is not attained through a high suction pressure in comparison with those which are found on diabase. In general values obtained in the suction pressure measurements in the diabase area are higher than those in the limestone area. In the opinion of the present authors there are not sufficient data available to make a definite conclusion. Probably species growing on limestone may develop a higher suction pressure under more severe circumstances than are found on the mentioned time. This is suggested by some stray observations at the very end of the dry season. Here, values of over 60 atmospheres were measured in *Coccoloba*, *Antirrhoea* and *Bourreria* growing on limestone.

Seeing that measurements made of the soil humidity show the limestone soil is more humid than that of diabase, as well as the indication that plants growing on limestone may develop a high suction pressure, it was supposed that the greater humidity of the limestone-soil was the result of a greater water capacity due to a better developed clay-complex. On the other hand the water capacity of diabase soil would be lower. Reason for this hypothesis was the granulometric composition of the soils derived from the three main geological formations in Bonaire (Westermann and Zonneveld, 1956) as well as the investigation of Hamilton and Sesseler (1945) on the soils of the West Indies. An analysis of two samples taken from Siberie and Malpais gave the following results:

	Siberie	Malpais
$CaCO_3$	2.6 %	2.0 %
Material finer than 2 μ as percentage of the mineral material smaller than 2000 μ	50 %	30 %
Humus content	7.7 %	10.4 %
Material 2000 μ	99 %	80.9 %
*p*H	8.1 %	7.4 %

The composition of the material smaller than 2000 μ is given in Fig. 8. From this it can be seen that the fraction smaller than 2 μ, which is the most important factor in the formation of the clay complex, is appreciable higher in limestone than in diabase. In the humid climates clay soils, so soils with a fine texture and with a high water capacity, provide moister habitats than soil with a coarse texture such as sandy soils. In arid regions, however, it is quite contrary (Walter, 1932, 1960, 1964). The fact must be emphasized that the soil on limestone plateaux is only found in fissures and rock

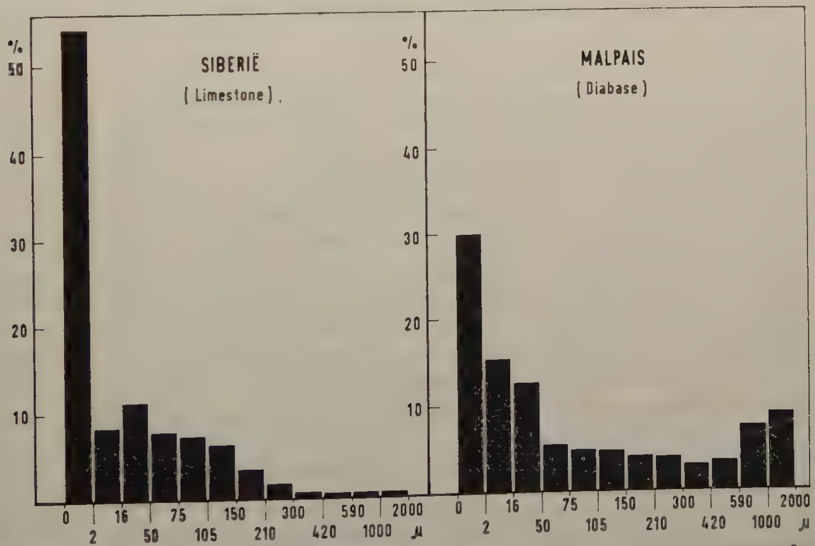

Fig. 8. Granulometric composition of the fractions smaller than 2000 μ of two soil samples taken at Siberie (limestone) and Malpais (diabese).

crevices so that only the upper layer can strongly dry out, while the deeper layers, approximately beneath 20 cm, are entirely protected against evaporation. The presence of a more luxuriant vegetation on limestone plateaux in this arid area must therefore be seen as a further example of what WALTER (1960, 1964) indicates as 'Das Gesetz der relativen Standortskonstanz und des Biotopwechsels' the 'Law of relative constant environment through changes of habitat'.

This might be an explanation for the phenomenon that species restricted to the limestone plateaux in this area are found on non-calcareous soils in other parts of the West Indies where the amount of precipitation is appreciable larger. It is also characteristic for those parts of the Seroe Christoffel where e.g. *Coccoloba swartzii* and *Metopium brownei* are found in large numbers that they have a higher water content in the soil than the diabase area (Stoffers unpubl.).

So the following picture can be given. In the diabase areas a shallow soil is found. Owing to the hilly character of these areas much of the rain water flows to the sea during and shortly after a shower. Only a part of the water soaks into the soil and even of this a portion is added to the ground water. (For geohydrological data reference should be made to MOLENGRAAFF, 1929 and WAGENAAR HUMMELINCK, 1940a, 1940b, 1953). Due to its low water capacity the soil becomes very easily saturated. The upper layers will dry out quickly after the rainy season through evaporation and water uptake by the herbs while the deeper layers are occupied by the roots of shrubs and trees. As a result, shortly after the last shower the soil water at the disposal of the plants is exhausted. Seeing that the coarse texture does not cause a rapid water succession the drought will be experienced by the plant very soon. This results in temporary wilting which slowly grades over into permanent wilting and leaf-abscission.

On the limestone plateaux, however, the case is entirely different because all the water disappears into the cracks and holes of the porous rocks in which a soil with a high water capacity is found. This soil becomes saturated and the superfluous water adds on to the groundwater. After the last showers the water content in the upper layers decreases considerably due to evaporation and also to use by the herb layer. But the greatest part of the added water will come at the disposal of the plants. Thus there is sufficient water available all the year round for plants whose roots grow to deeper depths or those plants rooting more superficially but capable to develop a higher suction pressure. Moreover this water is used very economically as the greater part of the plants already limit their transpiration at a small loss of water. Furthermore trees with a deep growing root system can slightly make use of the cavern water as can be seen for instance in the caves near Fontein (Bonaire).

It must be emphasized that the picture concerns only the shrub and tree vegetation. Concerning the herbs in the limestone soil the hydrature is reduced more severely by the high suction pressure of the clay in the upper layers of the soil.

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A NEW SPECIES OF STICHOTHAMNION (RHODOPHYTA) FROM THE WEST INDIES

M. VROMAN

(*Department of Botany, Free University, Amsterdam*)

(*received November 2nd, 1965*)

The genus *Stichothamnion* (*Rhodomelaceae*) was described by Børgesen in 1930, on the basis of material from the north western coast of Gran Canaria (Canary Islands).

During our investigation of marine algae collected from the Netherlands Antilles it appeared that on St. Eustatius (Lesser Antilles) an unknown species was gathered, that also has to be placed in the genus *Stichothamnion.* This material was of sufficient quality to allow a complete description of the species.

Stichothamnion antillarum nov. spec.

Frons dorsiventralis, 4–9 mm alta.
Surculus 85–110 μ latus, articulis 50–145 μ longis, ca 10 cellulas pericentrales continentibus.
Rhizoidea ex cellulis pericentralibus orta, usque ad 400 μ longa, 17–23 μ lata, 1–4 ex eodem articulo.
Ramuli erecti plus minusve subdichotome divisi, in parte basali et in parte media 80–115 μ lati, articulis 55–110 μ longis.
In superiori parte ramulorum trichoblasta simplicia, ca 19–27 μ lata, 310–1200 μ longa.
Tetrasporangia 42–50 μ lata, 38–42 μ longa.
Corpuscula antheridiorum subcylindrica, pedicellata, 190–260 μ longa, 40–60 μ lata.
Cystocarpia urceolata, 327–378 μ longa, 258–327 μ lata.
Type: West Indies, St. Eustatius, Back off Bay, on andesitic rocks, 21 V 1958.
leg. M. Vroman (herbarium of the Free University, Amsterdam; isotype Rijksherbarium, Leiden).

On the southern coast of St. Eustatius a remarkable geological formation, known as Sugarloaf and White Wall, is found, resting in a sloping position against the southern incline of the Quill vulcano. At the foot of this formation, over a length of about 100 m, the coastal line is formed by small boulders of andesitic origin. (Fig. 1). Normally the coast is strongly exposed to the prevaling eastern winds.

In the littoral zone, constantly washed by the waves, we find a close, mosslike algal growth in which the following species could be recognized:

Polysiphonia ferulacea, *Lophosiphonia cristata*, *Spyridia aculeata*, *Laurencia papillosa*, *Laurencia microcladia*, *Dictyota ciliolata*, *Dictyota dentata*, *Herposiphonia tenella*, *Padina vickersiae* and *Pocockiella variegata*. In this vegetation *Stichothamnion antillarum* is found.

Its growing place shows a remarkable likeness to that of *Stichothamnion cymatophilum* on the Canary Islands. Macroscopically it is difficult to distinguish *Stichothamnion antillarum* from *Lophosiphonia cristata* and *Polysiphonia ferulacea*, both species that are very common in this place.

Like *Lophosiphonia cristata Stichothamnion antillarum* shows a marked dorsiventrality. The plant has a creeping rhizome-like stem, fixed to the substrate by numerous small rhizoids. From the dorsal side 4–9 mm tall branchlets are formed, while the rhizoids are formed along the ventral side of the rhizome, 1–4 rhizoids from each segment. These rhizoids originate from the pericentral cells and have a length of up to 400 μ, but they are usually somewhat shorter (Fig. 4). At their ends small hapters are formed, by which they are fixed to the boulders. The diameter of the rhizoids is 17–23 μ. The walls are very thick and the lumen therefore is usually very narrow, 2–4 μ.

The rhizome grows in length by means of a large apical cell, from the basal end of which narrow flat cells are cut off. These divide in a central cell and about 10 pericentral cells. The fullgrown rhizome has a diameter of about 85–110 μ. The length of the segments is variable, 50–145 μ.

The branching of the rhizome takes place in the same way as described by Børgesen (1930) for *Stichothamnion cymatophilum*.

The apical cell is divided by a curved wall into a small disc like cell, which forms a new apical cell, and a larger cell below (Fig. 2a, b). Both cells function as an apical cell and from their basal end narrow disc like cells are cut off, which divide into central and pericentral cells. The filaments, formed in this way, divergate, and thus two branches are formed.

On the upper side of the rhizome the erect branches develop, usually after every 4–6 segments. They are endogenous in origin and grow, just like the rhizome, by means of a large, conical apical cell. The diameter of the erect branches is approximately the same over their whole length, 80–115 μ, and they are not narrowed at their base (Fig. 3). The segments have a length of 55–110 μ and possess 10–11 pericentral cells (Fig. 2j).

After the branchlets have reached some length they form trichoblasts. From the apical cell a segment is cut off by an oblique curved wall. Then a second wall is formed, almost perpendicular to the first. In this way a new apical cell is formed from which the trichoblast develops (Fig. 2e–h). First a number of short cells is formed; afterwards these cells lengthen and become colourless (Fig. 7). The trichoblasts are placed in an irregular spiral. In the older parts of the plant the trichoblasts die away. The trichoblasts can reach a length of 310–1200 μ, the diameter at their base is 19–27 μ; towards

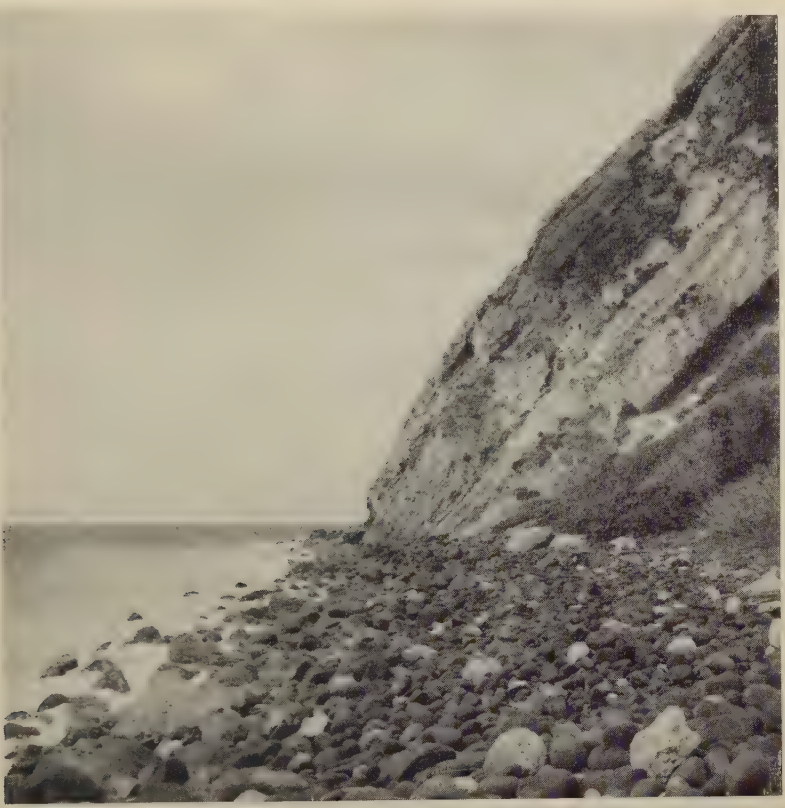

Fig. 1. St. Eustatius, growing place of *Stichothamnion antillarum* nov. spec. at the foot of Sugar Loaf and White Wall.

PLATE I

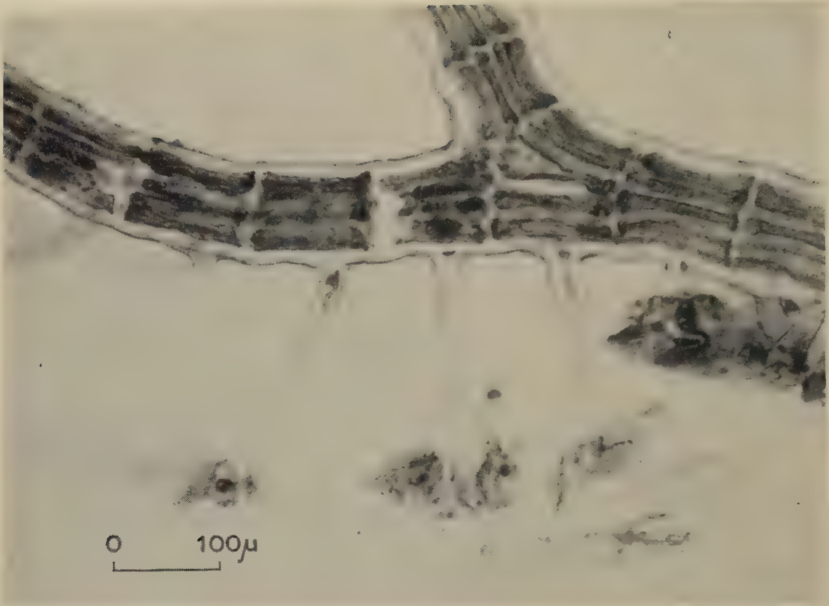

Fig. 4. *Stichothamnion antillarum* nov. spec., part of a creeping stem with rhizoids.

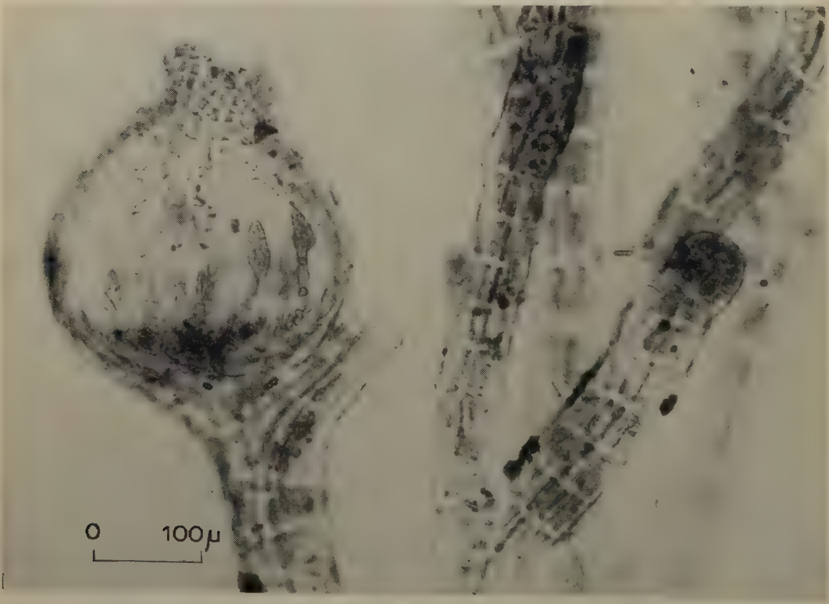

Fig. 5. *Stichothamnion antillarum* nov. spec., female plant with cystocarps.

PLATE II

PLATE III

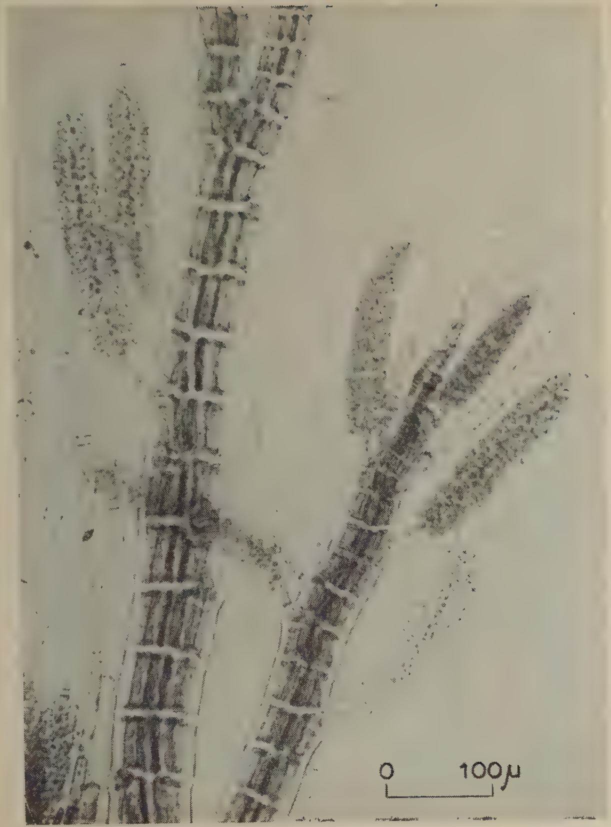

Fig. 6. *Stichotamnion antillarum* nov. spec., male gametophyte with antheridial bodies.

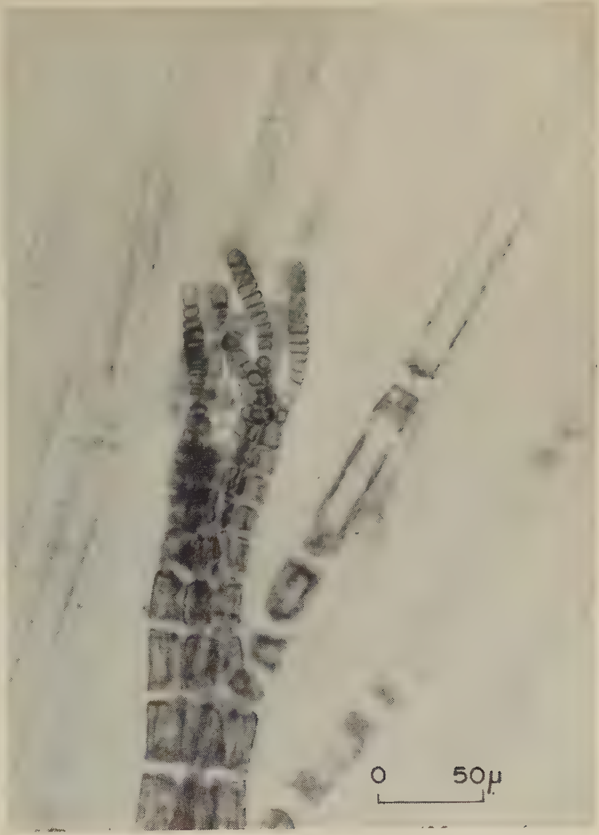

Fig. 7. *Stichothamnion antillarum* nov. spec., trichoblasts.

PLATE IV

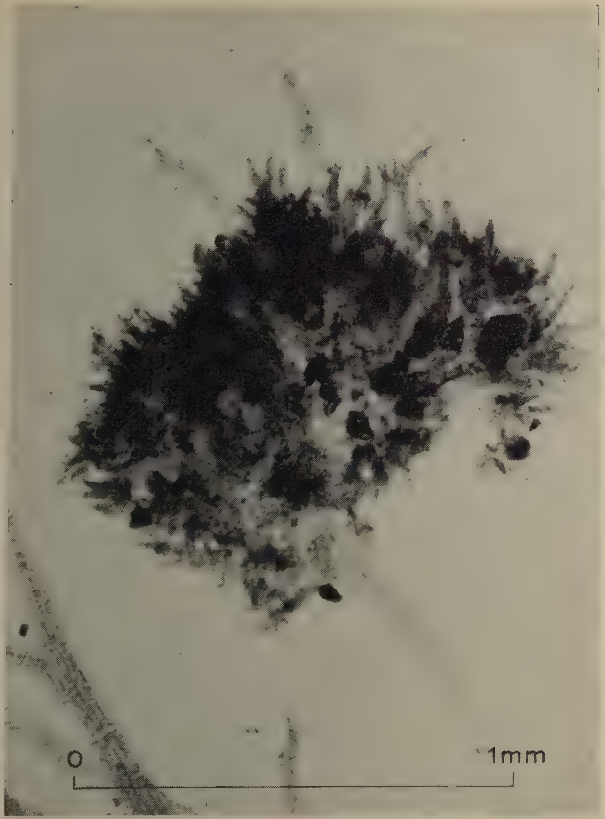

Fig. 8. *Stichothamnion antillarum* nov. spec., remarkable growths, possibly caused by a parasitic organism.

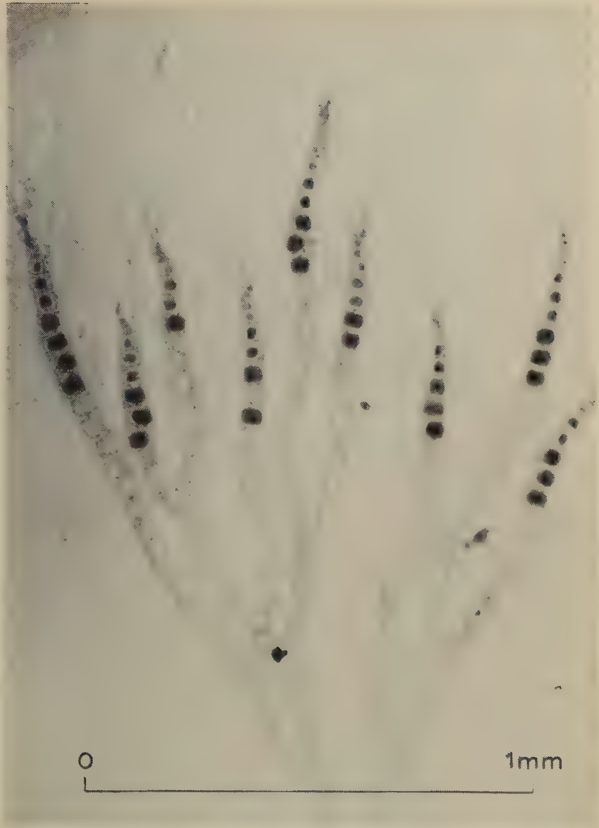

Fig. 9. *Stichothamnion antillarum* nov. spec., tetrasporophyte.

their tips the diameter is smaller, about 11.5 μ. The cells of the fullgrown trichoblast have a great length, to about 210 μ.

The greater part of the material from St. Eustatius consists of tetrasporophytes, but male and female plants were also found. The length of the erect branches varies from 4–9 mm. There are no differences in length between the tetrasporophytes and the gametophytes. The branching of the fullgrown plants is subdichotomous.

The tetrasporangia are formed in an irregular spiral in the upper part of the erect branches, one in each segment (Fig. 9). The sporangia have a length of about 42 μ; usually they are somewhat broader than long, 42–50 μ.

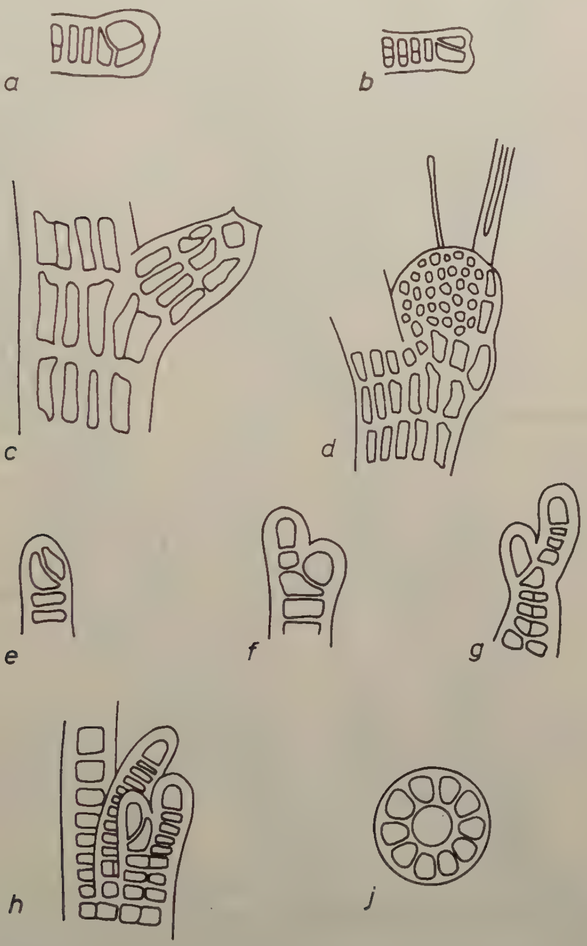

Fig. 2. *Stichothamnion antillarum* nov. spec. a–b, branching of the rhizome; c, development of the procarp; d, young cystocarp; e–h, development of trichoblasts; j, tranverse section of an erect branch of the thallus.

The antheridial bodies are formed by the trichoblasts of the male plants (Fig. 6). The two lowermost cells of the trichoblast remain sterile, and form the stalk of the antheridial body. At the tip one or two cells also can remain sterile. The young trichoblast, which is going to form the antheridial body, consists in the beginning, just like a sterile trichoblast, of a row of short cells. Very soon these

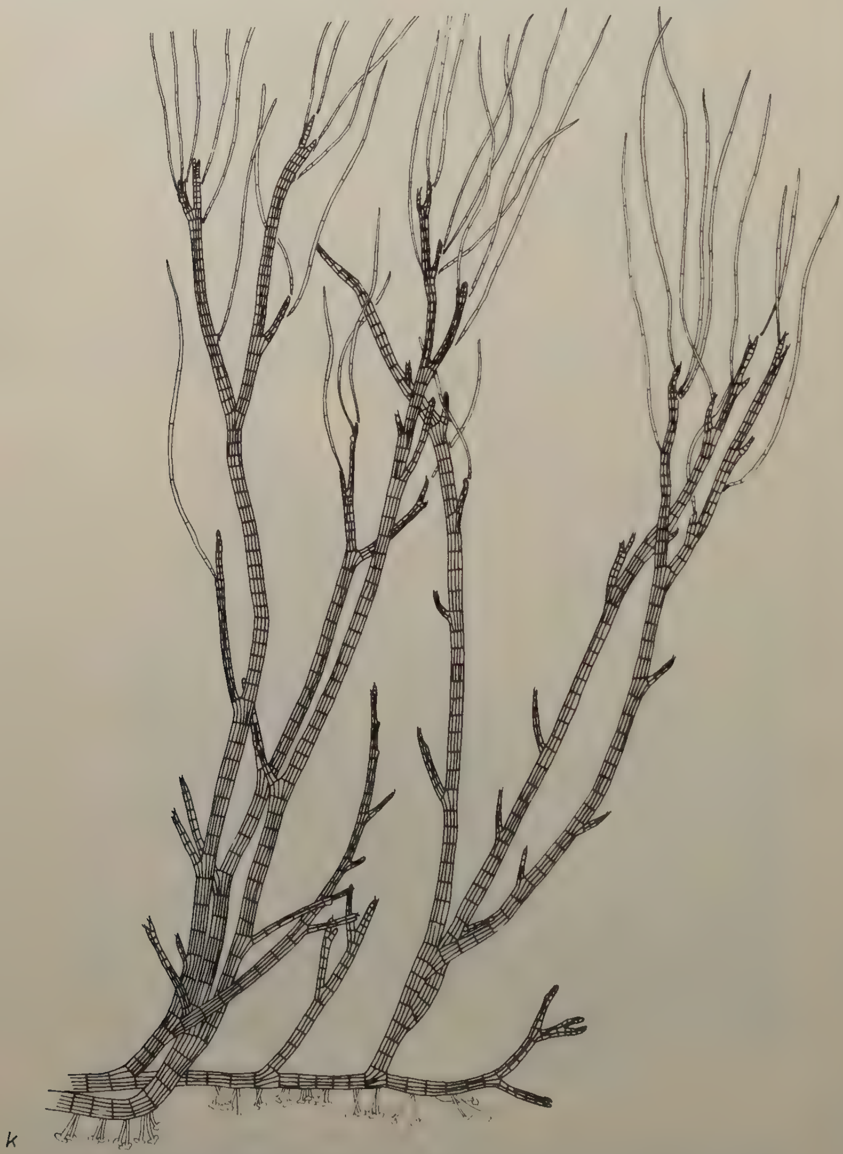

Fig. 3. *Stichothamnion antillarum* nov. spec. part of a young sterile plant.

cells are divided into central and pericentral cells, from the latter the antheridia are formed after several divisions. The central cells form a percurrent row through the antheridial body. The fully developed antheridial bodies are subcylindrical in shape, 190–260 μ long and 40–60 μ in diameter.

On the male gametophytes, and also on one or two tetrasporophytes several remarkable growths were found, not unlike the formations caused by parasitic microorganisms in the higher plants (Fig. 8). Their diameter is about 1 mm.
The growths are formed by a very close branching of *Stichothamnion*. Trichoblasts remain very short or are not formed at all. I did not find the cause for these growths. A fungus is possibly the reason.

The female plants, of which only two were found, are subdichotomously branched and the cystocarps are formed on the trichoblasts in the upper part of the plants. The two lowermost segments of a trichoblast become plurisiphonous, the uppermost of these two segments forms the procarp (Fig. 2c, d). During the development of the cystocarp the sterile part of the trichoblast drops off. When mature the cystocarp is urceolate, with a rather long neck in which an ostiole is formed (Fig. 5). From 5 ripe cystocarps the length varied between 327–378 μ, their diameter between 258–327 μ.
The carpospores are variable in form, oval to irregular.

From the description given above it is clear that the plant from St. Eustatius belongs to the genus *Stichothamnion*.
The organisation of the vegetative plant and the formation of the reproductive organs show a marked similarity to that of *Stichothamnion cymatophilum*, as described by Børgesen (1930). But there are also several distinct differences. The measurements of the material from St. Eustatius are larger than from *Stichothamnion cymatophilum* and also the form and insertion of the young erect branches is quite different. For these reasons it seems justified to distinguish a new species, which we have named *Stichothamnion antillarum*.

ACKNOWLEDGMENTS

The author is highly indebted to Mr. H. Cook, M.S.A., for correcting the English text, to Dr. C. van den Hoek and Mrs. van den Hoek for their help with the latin diagnosis, to Mr. C. van Groeningen for preparing the microphotographs and to Mr. G. W. H. van den Berg for drawing the figures.

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THE LINDSAEOID FERNS OF THE OLD WORLD
I. NEW CALEDONIA

K. U. KRAMER

ILLUSTRATIONS BY W. H. A. HEKKING

(Botanical Museum and Herbarium, University of Utrecht)

(received November 19th, 1965)

1. Introduction and phytogeographic notes

The present paper is the first of a series of regional revisions of the Old World Lindsaeoid ferns centering around a revision of the group in the Flora Malesiana area where the largest number of species occurs. In the few cases where modern revisions are already available the present author's contribution will be limited to critical and additional notes; otherwise they will be in the nature of monographic treatments, although widespread species will, of course, as a rule not be described more than once.

The botanically isolated position of New Caledonia is well-known, and most floristic phytogeographers agree in regarding it as a separate floristic region (e.g. Good, 1947; Van Balgooy, 1960). Endemism is high in the ferns as well as in the flowering plants, although the number of endemic fern genera is very small (Brownlie, 1965). In the absence of a comprehensive modern fern flora I am unable to quote any reliable figures. The last paper dealing with the New Caledonian fern flora as a whole by Fournier (1873) is nearly 100 years old. Later contributions were made notably by Copeland (1929b), Christensen (in: Däniker, 1932), and Guillaumin (1962–1964). Christ (1910), on the basis of Fournier's (1873) data, reported 259 species, 86 endemic, but stated that Fournier's species concept was apparently too narrow (p. 234), which I can confirm for the *Lindsaea* group, as shown by the synonymy in the present paper. On the other hand, additional species have been found or distinguished since. A more important factor limiting our knowledge of endemism in the New Caledonian ferns (and other plants) is, I think, the poor state of knowledge of the Melanesian flora, particularly of the Solomon Islands. The exploration that is now in progress in this archipelago may be expected to furnish important additional data.

As far as our present knowledge goes, 14 species of Lindsaeoid ferns occur in New Caledonia; 8 of them are endemic. (The Isle of Pines and the Loyalty Islands form part of the New Caledonian floristic region. The Isle of Pines is not considered separately here, and I have seen no collections of ferns from the group under discussion from the Loyalty Islands.) A discussion of their affinity should not only deal with the non-endemics but also include data on the distribution of the relatives of the endemic species. In the present group this is not an easy task as some of them occupy rather isolated positions.

The monotypic section *Davalliastrum* is very peculiar in the genus *Lindsaea* and not very close to any other group. In my opinion it is near the common source of the genera *Lindsaea*, *Tapeinidium*, and *Sphenomeris*, and it can be assigned only with difficulty to a genus (see p. 569). *Lindsaea vieillardii* has no close relatives but its affinities seem to be with *L. ensifolia*. *L. nervosa*, *L. prolongata*, and *L. rufa* form a natural group near *L. ensifolia* and *L. heterophylla* in *Schizoloma*, treated as a genus by some modern authors (HOLTTUM, 1957; BROWNLIE, 1961), sometimes under the superfluous name *Schizolegnia* (TARDIEU-BLOT, 1958), and maintained by myself (1958) as a subgenus; I now prefer to treat it as a section, with Holttum's circumscription (see p. 571). *Lindsaea francii* belongs to a group of closely related Malesian species. *Sphenomeris angustifolia* seems to belong near the very widespread gerontogean *Sph. chinensis* which also occurs in New Caledonia; *Sph. alutacea* is probably related to an E. Malesian-W. Pacific species. The distribution of the non-endemic species is stated in the taxonomic treatment; there is an Australian-New Zealand element (2 spp.), a South Pacific element (2 spp.), and a general paleotropical element (2 spp.).

When the assortment of Lindsaeoid ferns of New Caledonia is compared with that of other, physiographically ± similar islands in the tropical parts of the Pacific, we find a striking absence of the group *Lindsaea* subgenus *Odontoloma* which extends far into the Pacific with some very widespread species, e.g. *L. repens* (*macraeana*) to Hawaii, *L. rigida* to Tahiti. Other examples might be cited. This peculiarity New Caledonia shares to some extent with tropical Australia.

2. ECOLOGY AND DISTRIBUTION ON THE ISLAND

Many collections are without or with scanty ecological data. If any, they are summed up under the species.

Equally little can be said about the distribution in New Caledonia. The localities from which most species are known are concentrated in the South, but this is presumably due to the location of the capital in that part of the island.

3. MATERIALS; ACKNOWLEDGEMENTS

The herbaria in which the specimens are located that served for this study are cited with their standard abbreviations now in general use. I am greatly indebted to the Directors and Curators of these herbaria who sent their material on loan or permitted me to study it in place. My particular thanks go to Mme. M. Tardieu-Blot, Laboratoire de Phanérogamie, Muséum National d'Histoire Naturelle, Paris, for giving me access to the very rich New Caledonian collections in the herbarium of that institute and for generously giving some valuable duplicates to the Utrecht herbarium. The time spent at Paris was

unfortunately insufficient to study all the material there, and in the case of common species the citations from that herbarium are therefore incomplete.

A word of caution about the numbers of Franc's, and, to a lesser extent, Vieillard's New Caledonian specimens seems to be in place. They were apparently sorted to species and then numbered long after they had been collected, and a certain number on the label expresses some botanist's opinion on the species the specimen belongs to, rather than a particular place and date of the collection. These numbers are cited below with quotation marks.

4. TAXONOMIC PART [1]

Key to the genera (based on New Caledonian species):

1. Lamina simply pinnate or bipinnate with a conform terminal pinna . . . . *Lindsaea*
— Lamina decompound, i.e., at least bipinnate and without a conform terminal pinna 2
2. Ultimate divisions cuneate or linear; indusia attached at the sides for at least half their width . . . . *Sphenomeris*
— Ultimate divisions not cuneate or linear, or, if so, the indusium laterally quite free . . . . *Lindsaea*

Sphenomeris Maxon

Key to the species:

1. Primary pinnae with a terminal pinnule similar to the lateral ones . . . . 3. *Sph. alutacea*
– Upper pinnules reduced, confluent, the primary pinnae without a terminal pinnule 2
2. Larger sori on 4–8 vein-ends . . . . 4. *Sph. deltoidea*
– Sori on 1 or 2 vein-ends 3
3. Ultimate segments rigid, with revolute margin; scales ovate, with acicular apex; spores trilete . . . . 1. *Sph. angustifolia*
– Ultimate segments not rigid, the margin not revolute; scales entirely acicular; spores monolete . . . . 2. *Sph. chinensis*

1. **Sphenomeris angustifolia** (Bernh.) Brownlie, Trans. Roy. Soc. N. Zeal. 87: 196, 1959. Basionym: *Lindsaea angustifolia* Bernhardi, Schr. Akad. Erfurt 14, fig. 6, 1802, based on: *Adiantum clavatum* Forster, Flor. Ins. Austr. Prodr. 83, 1786, non L., 1753 [which is *Sph. clavata* (L.) Maxon]. – *Odontosoria angustifolia* (Bernh.) C. Chr., Ind. Fil. 464, 1906. – *Stenoloma angustifolium* (Bernh.) C. Chr., Ind. Fil. Suppl. III: 173, 1934. – *Davallia forsteri* Carruthers ex Seemann, Fl. Vit. 339, 1873, nom. invalid. in synon. – *Microlepia forsteri* (Carr. ex Seem.) Armstrong, Trans. N. Zeal. Inst. 13: 364, 1881. – Type: a specimen without data numbered 459 (BM!).

Lindsaea scoparia Mettenius, Ann. Sci. Nat. IV. 15: 64, 1861. – *Davallia scoparia* (Mett.) Hooker in Hooker and Baker, Syn. Fil. 1st ed. 101, 1867. – *Microlepia scoparia* (Mett.) Carruthers ex Seemann, Fl.

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[1] For the terminology, see KRAMER (1957).

Vit. 340, 1873. – *Schizoloma scoparium* (Mett.) Kuhn, Chaetopt. 346, t. 1 fig. 1, 1882. – *Odontosoria scoparia* (Mett.) Diels in Engler und Prantl, Nat. Pfl. I^4: 215, 1899. – *Sphenomeris scoparia* (Mett.) Copeland, Univ. Calif. Publ. Bot. 14: 366, 1929. – *Stenoloma scoparium* (Mett.) C. Chr., Ind. Fil. Suppl. III: 173, 1934. – Lectotype: Vieillard 1550, Balade (P!).

Not *Davallia remota* Kaulfuss, cited by Duperrex (teste FOURNIER, 1873), which was described from Hawaii and belongs to the next species.

This species in habit closely resembles the narrower form of *Sph. chinensis*; the principal differences are given in the key. Scales fuscous, to 2 mm long, to nearly 1 mm wide at base. Sori binerval; indusium pale, 0.4 mm broad, not quite reaching the margin, the sides attached for about half their length, sometimes flanked by a small tooth on the latero-apical extremity of the segment. Spores medium brown, trilete, ca. 35 μ. **Fig. 1A, 3A**

Distribution: endemic.

Ecology: by mountain streams, torrents, etc., 400–500 m. The plant has the appearance of a rheophyte.

Selected citations:

Vieillard 1550, Balade (lectotype of *L. scoparia*, P; isotypes B, K); id. 1550–1551–1552, Wagap (B, K, L, P, Pic.-Ser.); Franc 1428, Tao (P); Sarasin 7, above Oubatche (P, Z); Le Rat 1115, s.l. (P).

2. **Sphenomeris chinensis** (L.) Maxon, Jo. Wash. Acad. Sci. 3: 144, 1913. Basionym: *Trichomanes chinense* L., Spec. Plant. 2: 1099, 1753. – Type: Osbeck s.n., China (S-PA!).
Adiantum chusanum L., Spec. Plant. 2: 1095, 1753. – *Sphenomeris chusana* (L.) Copeland, B. P. Bishop Mus. Bull. 59: 69, 1929. – Type: coll.?, China (LINN!).
Adiantum tenuifolium Lamarck, Encycl. I: 44, 1783. – *Davallia tenuifolia* (Lam.) Swartz, Schrad. Journ. 1800^2: 88, 1801; Fournier, Ann. Sci. Nat. V. 18: 338, 1873. – *Lindsaea tenuifolia* (Lam.) Mettenius, Ann. Sci. Nat. IV. 15: 64, 1861. – Type: Sonnerat s.n. from 'India' (P!).
Trichomanes cuneiforme Forster, Flor. Ins. Austr. Prodr. 85, 1786. – *Davallia cuneiformis* (Forster) Swartz, Schrad. Journ. 1800^2: 87, 1801. – Type: a specimen without data, possibly from New Caledonia, numbered 306 and 469 (BM!).

It is not necessary to give here a description of this well-known species which is very widespread in the tropical and warm-temperate parts of the Eastern Hemisphere, but is apparently absent from Australia and New Zealand.

The arguments for adopting the name *Sphenomeris chinensis* instead of *Sph. chusana*, mostly used in recent literature, will be explained elsewhere, where the full synonymy will also be given.

Ecology: open places, by trails and rivulets, to at least 800 m. Described as psammophilous by Virot.

Selected citations:

Franc '667', Dumbéa (BRI, K, MICH); id. '667', Ouaouo (BRI, GH, K, L, US); id. '667', Col d'Amieu, La Toa (B, BRI, GH, MICH, US, Z); Virot 736, Hienghène (A); Le Rat 556, Mt. Mou (B); Vieillard 1548, Wagap (B, GH, L); McKee 2532, Hienghène (U); id. 3171, Vallée de Thy (US).

3. **Sphenomeris alutacea** (Mett.) Copeland, Univ. Calif. Publ. Bot. 14: 365, 1929. Basionym: *Lindsaea alutacea* Mettenius, Ann. Sci. Nat. IV. 15: 63, 1861. – *Schizoloma alutaceum* (Mett.) Kuhn, Chaetopt. 346, 1882. – *Stenoloma alutaceum* (Mett.) C. Chr., Ind. Fil. Suppl. III: 173, 1934. – Lectotype: Vieillard 1554, Kanala (P!).

Rhizome rather long-creeping, 2–3 mm in diam., with an internal sclerotic strand; scales lustrous, dark reddish brown to castaneous, with 3 rows of cells at the base and a very long apex of one row of cells, up to 5 mm long. Petioles close to rather remote, fawn-coloured, abaxially rounded to obtusely bi-angular, slender, up to ca. 20 cm long, 1–1½ × as long as the lamina. Lamina subcoriaceous to coriaceous, drying brown, narrowly oblong, bipinnate or tripinnate at base, the apex gradually of simpler structure; pinnate or bipinnate pinnae ca. 6–9 to a side, obliquely ascending, short-petiolulate, axes slender. Ultimate pinnules triangular-cuneate, the larger ones irregularly, asymmetrically, and shallowly incised from the apical margin, about 10 mm long and 6 mm wide, the smaller ones relatively narrower and often entire, esp. when fertile; margin sclerotic, laterally ± distinctly revolute. Upper pinnules of pinnae little reduced, not confluent. Pinnae and lamina with a terminal, often relatively broad pinnule. Veins immersed to somewhat prominulous beneath, to 4 times furcate. Sori on (1—) 2–6 (—10) vein-ends, single on smaller, entire pinnules, larger pinnules with a sorus to a lobe; indusium rigid, subentire to entire, the sides at least for ½ of their length attached, ca. 1 mm wide, not quite reaching the margin. Spores medium brown, trilete, subglobose, ca. 30–35 μ. **Fig. 3C**

Distribution: endemic; apparently frequent.

Ecology: by creeks and torrents and in dry stream-beds; reported by some to have a preference for ferritic soil. From 50–800 m.

Selected citations:

Vieillard 1554, Kanala (P, lectotype; isotype K); id. '1546', Yaté (P, paratype; B); id. '1546', Unia R. (P, L); id. '1546', Mt. Dore (B, GH, L); Schlechter 15192, Ngoye (B, BO, GH, HBG, K, L, P, Z); Franc '540', Dumbea R. (B, BRI, P, US); id. '540', Dzumac (B, GH, MICH, P); id. '540', Baie du Sud (BRI, Z); Le Rat 82, Mt. Dzumac (BO, P); Sarasin 161, Ngoy Valley (P, Z); Rohrdorf 157, Baie du Sud (Z); McKee 1086, Mt. Dore (K, U); id. 2057, Plaine des Lacs (U).

A clear-cut species, probably related to *Sph. retusa* (Cav.) Maxon which occurs in eastern Malesia, east to the Solomon Islands. The terminal pinnules are quite distinctive.

4. **Sphenomeris deltoidea** (C. Chr.) Copeland, Univ. Calif. Publ. Bot. 14: 366, 1929. Basionym: *Lindsaea deltoidea* C. Christensen, Ind. Fil. 393, 1906, based on: *Lindsaea elongata* Labillardière, Sert. Austro-Caled. 6, t. 9, 1824, non Cavanilles, 1802. – *Schizoloma elongatum* (Lab.) Kuhn, Chaetopt. 346, 1882. – *Stenoloma deltoideum* (C. Chr.) C. Chr., Ind. Fil. Suppl. III: 173, 1934. – Type: Labillardière s.n., New Caledonia (P!).

Rhizome rather long-creeping, with an internal sclerotic strand, in adult plants stout, 7 mm in diam.; smaller, not full-grown plants which are often fertile with much thinner rhizome. Scales castaneous, tot 4 mm long, with 3–4 rows of cells at the base, with a long apical part of 1 row of cells. Petioles rather remote, fawn-coloured, abaxially terete, stout, 3–6 mm thick, 15–45 cm long, about as long as the lamina. Lamina ovate or deltoid, 1½–2 × as long as broad, subcoriaceous or coriaceous, usually drying brown, bipinnate + pinnatifid or tripinnate; primary rachis somewhat flexuous. Pinnae to ca. 10 to a side, ovate to rhombic-deltoid, petiolulate, acuminate, the lower ones sometimes remote, the upper ones gradually and strongly reduced, no conform terminal pinna present. Pinnules rather remote, narrowly rhombic-deltoid, acuminate or acute, in larger pinnae 7–10 to a side, the upper ones gradually and strongly reduced, confluent; pinnules of larger pinnae pinnatifid or pinnate at base, with rhombic or ovate-oblong, pinnatilobate secondary pinnules up to ca. 1½ cm long and 1 cm wide; upper part of pinnules always pinnatifid, with upward gradually reduced segments. Margin often sclerotic and then somewhat revolute. Veins somewhat prominulous or immersed but evident, 2–3 × forked in the larger lobes. Ultimate lobes truncate, slightly narrowed to apex or almost parallel-sided, the larger ones 3–5 mm wide at apex, the sinuses between them narrow, acute. Sori mostly borne on all vein-ends of a lobe, on larger lobes 4–8-nerval, also borne on smaller lobes and sometimes extending nearly or quite to the apices of pinnae and pinnules. Indusium rigid, subentire, pale to medium brown, ca. ½ mm wide, almost reaching the margin but reflexed at full maturity. Spores pale brown, trilete, smooth, ca. 38–45 μ. (For an illustration of a sporangium, see Kramer, 1957, p. 120, fig. 18). **Fig. 3B**

Distribution: New Ireland, Solomon Islands; New Hebrides?

Ecology: in thickets and moist, open places, often by watercourses, 50–300 m; often on ferritic soil. Apparently common.

Selected citations:

Labillardière s.n.s.l. (P, type; isotype B); Vieillard '1545', Wagap (B, L, P); id. '1545', Unia (GH, K, P); Schlechter 14815, Yaouhé (B, HBG, K, L, P, Z); Sarasin 13, Oubatche (P, Z); Buchholz 1051, Mt. Dore (K, US); Rohrdorf 185, Baie du Sud (Z); Franc '358', Mt. Koghi (BRI, K, L, MICH, P, US, Z): id. '358', L'Hermitage (B, K, L, P, Pic.-Ser., U); id. '358', Plum (B, BRI, K, L, SING); McKee 4652, road to Montagne des Sources (U, US); C. Moore 3, Kanala (K); Däniker 1580, island Yandé (Z). Isle of Pines: Vieillard 164 (P); Milne 206 (K); McGillivray 33 (K); id. 747 (GH, K); Germain s.n. (B, K, P).

The closest relative of this distinctive species is probably *Sph. retusa* (see under the preceding species).

Lindsaea Dryander

Artificial key to the species:

1. Veins anastomosing, sometimes free in smaller lobes 2
– Veins quite free 4
2. Pinnules dimidiate . . . . 10. *L. harveyi*
– Pinnules ± equal-sided 3
3. Sterile margin coarsely serrato-dentate; sori strongly intramarginal . . . . 6. *L. vieillardii*
– Sterile margin crenate to subentire; indusium almost or quite reaching the margin (except when reflexed) . . . . 5. *L. ensifolia*
4. Lamina simply pinnate; shorter, spreading, sterile leaves always present beside the erect fertile ones, their pinnules sometimes incised 5
– Lamina bipinnate or more dissected; full-grown plants without sterile leaves, or these not appreciably different from the fertile ones 6
5. Axes dark; pinnules of sterile leaves sinuate . . . . 8. *L. linearis*
– Axes pale; pinnules of sterile leaves cleft . . . . 7. *L. dimorpha*
6. Upper pinnules strongly reduced, confluent to the pinna-apex; sori short, uni- or binerval 7
– Upper pinnules not strongly reduced, a large, free or almost free terminal pinnule (segment) present; fully fertile pinnules with longer sori 8
7. Lamina with a conform terminal pinna; pinnules dimidiate; spores trilete . . . . 9. *L. francii*
– Lamina without a conform terminal pinna; pinnules (ultimate segments) not dimidiate; spores monolete . . . . 1. *L. moorei*
8. Terminal pinnule linear, coarsely serrate; leaf-tissue herbaceous; veins immersed; sori strongly interrupted, the larger ones occupying the outer and part of the lateral margin of the pinnule-lobes, with very concave base . . . . 4. *L. prolongata*
– Terminal pinnule triangular to ovate-lanceolate, crenate, or serrate at base only; leaf-tissue subcoriaceous to coriaceous, with prominulous veins; sori long, little interrupted, or, if short, occupying only the outer margin of the pinnule-lobes 9
9. Terminal pinnule (segment) acute or acuminate; very few (or no) transitions at base of terminal pinna from pinnate lateral pinnae to lobed basal pinnules of terminal pinna, i.e., lamina almost (or quite) with a conform terminal pinna . . . . 3. *L. nervosa*
– Terminal segment obtuse; several transitions near lamina-apex from pinnate pinnae through very asymmetrically divided or basally asymmetrical pinnules to simple ones, i.e., no distinct, conform terminal pinna present . . . . 2. *L. rufa*

Section *Davalliastrum* (Fournier) Kramer, stat. nov. – *Lindsaea* (subdivision, without indication of rank; best regarded as subgenus) *Davalliastrum* Fournier, Ann. Sci. Nat. V. 18: 330, 1873. Lectotype species: *Lindsaea moorei* (Hooker) Fournier.

Fournier's characterization of this group is so brief, 'fronde decomposita', that its validity may be doubted. It also comprises species of what I regard as two genera, *Lindsaea* and *Sphenomeris*, and in the former of two sections, *Schizoloma* and *Davalliastrum*. Yet 6 of the 10 species belong to the group as defined here, although I regard them as forms of a single species.

Rhizome terrestrial, with a Lindsaeoid protostele but near the leafbases with an internal sclerotic strand; scales ovate, small, inserted on protuberances of the rhizome cortex (see fig. 5). Lamina decompound, free-veined; sori nearly always uninerval, terminal or subterminal on the lobes of the pinnately incised ultimate free divisions; indusium membranous, only attached at the (often convex) base, laterally free; spores monolete.

I have long hesitated before including this species in *Lindsaea*. It shows resemblance to *Sphenomeris* and *Tapeinidium*, particularly in the leaf-pattern and in the rhizome anatomy. Its laterally free indusia and the shape of its scales exclude it, however, from both genera; it may be related to *Sph. angustifolia* but is in my opinion closer to the group of species which I united (KRAMER, 1957) in the section *Pseudosphenomeris*. The insertion of the scales on mounds is unlike anything I have seen in *Lindsaea*; and monolete spores, not uncommon in the neotropical species, are very rare in the paleotropical ones. The solution to erect a new genus for it seems to have too little support; moreover it is undesirable in a group where the separation of the described genera already meets with difficulties. I therefore prefer to leave it in the most heterogeneous of the Lindsaeoid genera. I cannot agree with HIERONYMUS (1920) that its closest relative is *Tapeinidium denhamii* (Hooker) C. Chr.

1. **Lindsaea moorei** (Hooker) Fournier, Ann. Sci. Nat. V. 18: 336, 1873. Basionym: *Davallia moorei* Hooker, 2nd Cent. Ferns t. 53, 1861. – *Odontosoria moorei* (Hooker) Kuhn, Chaetopt. 346, 1882. – *Tapeinidium moorei* (Hooker) Hieronymus, Hedwigia 62: 13, 1920. – *Sphenomeris moorei* (Hooker) Copeland, Univ. Calif. Publ. Bot. 14: 366, 1929. – Type: Ch. Moore 5, Kanala (Canalla) (K!).
Lindsaea balansae Fournier, Ann. Sci. Nat. V. 18: 335, 1873. – Type: *Balansa* 1652, Messioncoué (P!).
Lindsaea campylophylla Fournier, Ann. Sci. Nat. V. 18: 335, 1873. – *Sphenomeris campylophylla* (Fournier) Tardieu, Am. Fern Jo. 48: 34, 1958. – Type: Balansa 854, nr. Daaoui de Ero (P!).
Lindsaea exilis Fournier, Ann. Sci. Nat. V. 18: 335, 1873. – Lectotype: Balansa 1650, between Ouailou and Couaoua (P!).
Lindsaea flavicans Mettenius ex Fournier, Ann. Sci. Nat. V. 18: 334, 1873. – *Tapeinidium flavicans* (Mett. ex Fourn.) Hieronymus, Hedwigia 62: 13, 1920. – Lectotype: McGillivray F 14, Kanala (P!).
Lindsaea mediocris Fournier, Ann. Sci. Nat. V. 18: 336, 1873. – Lectotype: Balansa 42a, Mt. Cougui (Koghi) (P!).
Davallia lenormandi Baker, Syn. Fil. 2nd ed. 471, 1874. – *Odontosoria lenormandi* (Baker) C. Chr., Ind. Fil. 465, 1906. – Lectotype: Deplanche 1 (herb. Lenormand), N. Cal., without loc. (K!).[1]

Rhizome short-creeping, 2–3½ mm in diam.; scales very dark brown, lustrous, to ⅔ mm long, with up to ca. 6 rows of cells at the base, the apical part of one row of cells rather short, apical cell

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[1] The names *L. mariae* Fourn. and *L. pancheri* Fourn., cited by GUILLAUMIN (1964), are *nomina nuda*.

glandular but often lost. Petioles close, abaxially terete to very obtusely bi-angular, reddish to blackish brown but not rarely the upper part and the adaxial side paler, stramineous or mottled, ca. 15–40 cm long, in large leaves 1½–3 × as long as the lamina, 1–2 mm in diam. Lamina very variable, chartaceous to coriaceous, ovate-oblong to subrhombic, triangular, or pentagonal, up to ca. 30 × 15 cm, bipinnate + pinnatilobate to tripinnate + pinnatipartite, drying pale brownish to dark green but mostly olivaceous. Primary rachis similar to the upper part of the petiole; secondary rachises abaxially terete, pale (sometimes abruptly so), like those of higher order upward increasingly green-margined. Primary pinnae obliquely ascending or the lower ones patent, short-petiolulate to subsessile; major pinnae mostly 3–5 to a side, the upper ones gradually reduced, of simpler structure, confluent into a pinnatifid, often acuminate leaf-apex. Basal pinnae the largest, often, especially in large laminas, strongly basitonically developed, then the outline of the lamina ± pentagonal. Pinnules and segments decurrent into the wings of the axes; apices of the pinnae (and pinnules in tripinnate leaves) like the apex of the lamina. Ultimate segments very variable, truncate-cuneate, obovate-cuneate, subrhombic-cuneate, 2–4 mm wide, or less often linear-cuneate, 1–2 mm wide, of very variable size depending on the specimen and the place in the lamina; margin not sclerotic, sometimes subrevolute, serrato-pinnatilobate to pinnatifid in larger segments. Veins pinnately branched, abaxially often pale and prominulous. Sori uni– (very rarely bi–) nerval, on the teeth of the ultimate segments, ½–1 (very rarely –2) mm long, ½ mm wide; indusium pale to medium brown, free at the sides, erose to cleft, not reaching the margin by less than its width to almost reaching it, not reflexed at maturity. Edge of lamina opposite the indusium not rarely erose or uni- or bicorniculate. Sporangia intermingled with numerous soral trichomes of one row of cells. Spores pale brown, monolete, bean-shaped to ellipsoidal, ca. 60 × 40 μ. (See also the description of the section).

Fig. 1B, 4A

Distribution: endemic (one coll. found as an admixture in a collection from Fiji, but probably not collected there).

Ecology: in open places, crevices of rocks, by watercourses and in forests, on ferritic and serpentine substrate, from c. 100–1050 m. There is probably some connection between the variability of this species and the fact that it is very euryoeceous. The finely dissected plants mostly seem to come from forests, but the ecological data are insufficient for definite conclusions.

Selected citations:

Balansa 1652, Messioncoué (P, holotype of *L. balansae*; isotypes P, 2 sh., B); id. 854, Daaoui de Ero (P, holotype of *L. campylophylla*; isotype P); id. 1650, between Ouailou and Couaoua (P, lectotype of *L. exilis*; isotypes P, 2 sh.); id. 42a, Mt. Koghi (P, lectotype of *L. mediocris*; isotypes P, B); Balansa 1651a, Prony (P, paratype of *L. mediocris*); Ch. Moore 5, Kanala (type, K); McGillivray F 14, Kanala (P, lectotype of *L. flavicans*); McKee 4690, Montagne des Sources (K, L, U, US);

id. 3534, Mt. Mou (P, U); Franc '360', Koghi (BRI, K, L, MICH, P, Pic.-Ser., US); id. '360', Mt. Dore (BRI, K, P, Z); Vieillard 1548 and 1549, Wagap (B, P); Sarasin 589, Yaté (P, Z); Schlechter 15046, Yaouhé (B, HBG, K, P, Z); id. 15344, Ngoye (Z), 15364, ibid. (B, K, P); id. 14955, Paita (B, K, L, P, Z); Guillaumin 10920, Rivière Bleue (Z); Virot 586, Plaine des Lacs (A). Isle of Pines: Pancher s.n. (B, K, P, paratypes of *L. flavicans*.).

BROWNLIE (1961) already emphasized the great variability of this species. With an ample series of material at hand, notably in the Paris herbarium, I am unable to find any reliable distinction between the, admittedly rather divergent, forms described as species by FOURNIER (1873). BROWNLIE (l.c.) referred *L. tenuifolia* Mettenius to this species, but it is a synonym of *Sphenomeris chinensis* (q.v.).

Section *Schizoloma* (Gaud.) Kramer, stat. nov. – *Schizoloma* Gaudichaud, Ann. Sci. Nat. 3: 507, 1824 (as genus). – *Lindsaea* subgenus *Schizoloma* (Gaud.) Hooker, Spec. Fil. I: 219, 1844; Kramer, Acta Bot. Neerl. 6: 271, 1957.–*Lindsaea* section *Pseudosphenomeris* Kramer, l.c., p. 165.

2. **Lindsaea rufa** Kramer, spec. nova. – *Schizoloma heterophyllum* (Dryander) J. Smith forma major 'Fournier'; C. Christensen, Beibl. Vierteljahrsschr. Naturf. Ges. Zürich 77: 20, 1932, based on *L. heterophylla* Dryander forma major Fournier, l.c., p. 331, 1873, which is in my opinion not intended as a formal description of a new forma but a critical note on the specimens.
Rhizoma breviter repens, 2 mm crassum, squamis angustis ferrugineis obtectum; petioli approximati, abaxialiter bi-angulares, rufescentes vel deinde brunnescentes. Lamina petiolo brevior, subcoriacea, bipinnata, pinnis pinnulisque obtusis, pinnulis superioribus sensim abbreviatis, pinnam terminalem lateralo-basalibus similem non efformantibus. Venae liberae, prominulae. Margo scleroticus, crenatus, incisionibus soros plerumque hinc inde interrumpentibus. Indusium rigidum, marginem non attingens.
Additional characters: scales lanceolate acuminate, up to 2 mm long, with up to 8 rows of cells at the base. Petioles ca. 12–35 cm long, about twice as long as the lamina, 1–1½ mm in diam., dull; rachis similar to the petiole, secondary rachises paler, abaxially subterete. Lamina rarely subtripinnate, ovate or oblong, 1½–2 × as long as wide, drying olivaceous-brown; pinnate pinnae in about 4 pairs, about as many lobed or simple ones above, progressively shorter from base to apex of lamina, the upper ones obovate-flabellate, ca. 1 cm long, scarcely confluent with the asymmetrically lanceolate terminal pinnule; pinnules of pinnate lateral pinnae 1–3 to a side, similar to the ones near the leaf-apex or the lower, largest ones more elongate. Costae soon evanescing in flabellate, more pronouncedly developed in lanceolate pinnae (pinnules); veins mostly twice forked. Margin stramineous or reddish, lobes subacute in sterile pinnules, flattish and separated by incisions up to ca. 1 mm deep in fertile pinnules. Sori usually occupying all vein-ends of fully fertile pinnules,

continuous in small, interrupted by the crenations in larger pinnules, there the longest ca. 1 cm long. Indusium stramineous. subentire, ca. 0.3–0.4 mm wide, falling short of the margin approximately by an equal distance, ± reflected at maturity. Spores pale brown, slightly tuberculate, trilete, ca. 27 μ. **Fig. 2C, 3D**

Type: Schlechter 15108, Ngoye (B).
Distribution: endemic.
Ecology: in forests, 100–1250 m (few data).

Specimens seen:
Franc 2039 p.p., s.loc. (MICH); id. 1393 p.p., Mt. Mou (BRI, K, MICH); Balansa 1602a, Mt. Humbold (P); Skottsberg 55, Montagne des Sources (S-PA); Vieillard 3354, Mt. Mou (B); Schlechter 15108, Ngoye (B, holotype; isotypes B, BM, BO, GH, HBG, K, L, Z).

The sclerotic margin, the firm texture, and the free veins distinguish this species readily from *L. heterophylla* with which it has been confused and which may be its closest relative. It may be even closer to *L. nervosa*; for the differences see the key.

3. **Lindsaea nervosa** Mettenius, Ann. Sci. Nat. IV. 15: 62, 1861, non Lindman, 1903. – *Schizoloma nervosum* (Mett.) Kuhn, Chaetopt. 346, 1886. – Type: Vieillard 1540, Mont Dore (P!).
Lindsaea macgillivrayi Carruthers ex Seemann, Fl. Vit. 337, 1873. – Type: McGillivray F 16, 'interior of New Caledonia' (BM!).
Lindsaea neocaledonica Compton, Jo. Linn. Soc. 45: 443, 1922. – Type: Compton 791, Mt. Koghi (BM!).

Rhizome rather short- to long-creeping, 1½–2 mm in diam.; scales rufous, narrow, to 2 mm long, with up to 3 rows of cells at the base and a long apical part of one row. Petioles close to remote, ca. 20–50 cm long, mostly exceeding the lamina, reddish brown (mostly dark), ± shining, abaxially terete or bi-angular upward, 1–2 mm in diam. Lamina subcoriaceous, or occasionally chartaceous or coriaceous, drying olivaceous to dark green, 15–40 cm long, 15–25 cm broad, oblong or in small leaves as broad as long, bipinnate or rarely subtripinnate, with 3–11 pinnae to a side and an almost or quite conform terminal one; primary rachis similar to the petiole, secondary rachises reddish brown, abaxially terete. Pinnae patent or obliquely ascending, subsessile to short-petiolulate, linear; upper pinnae, esp. in large leaves, somewhat or occasionally strongly shortened; larger pinnae commonly 10–15 × 2 cm, with ca. 20 pinnules to a side, rarely the basal pinnae with a basal basiscopic pinnate secondary pinna. Pinnules of variable shape but distinctly dimidiate: semi-elliptic or subovate and very obtuse to rhombic or caudato-acuminate. Basal pinnules scarcely or not, upper pinnules little reduced, none or 1 or 2 connected with the asymmetrically lanceolate or hastate, acute or acuminate, often pinnately lobed terminal pinnule (segment). Terminal pinna at base mostly with some enlarged, lobed pinnules forming a vestigial transition to the upper pinnae. Margin of pinnules

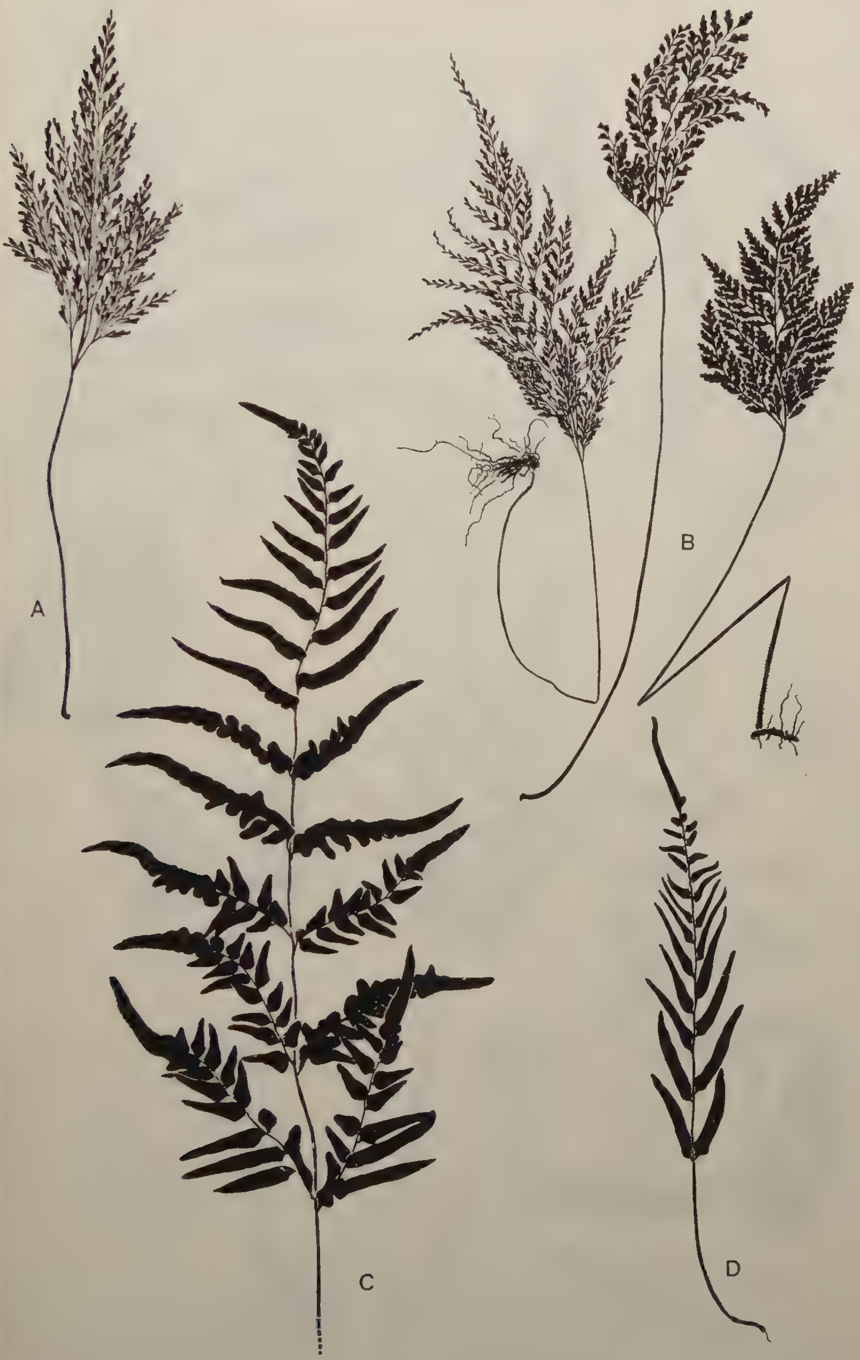

Fig. 1. A: *Sphenomeris angustifolia*. B: *Lindsaea moorei*, leaves from 3 different plants showing the variability. C, D: *Lindsaea ensifolia* ssp. *agatii*, two extreme forms.

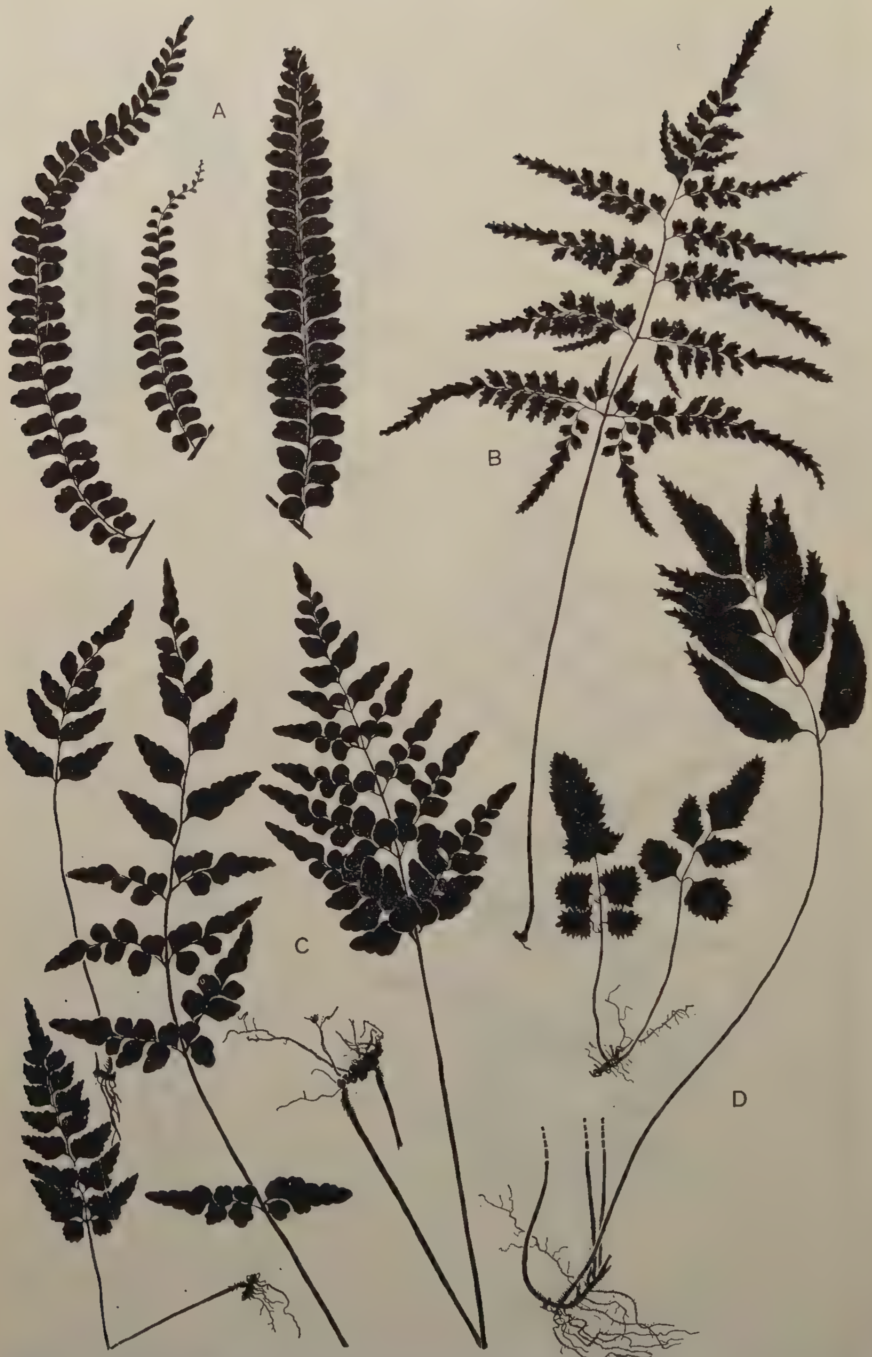

Fig. 2. A: *Lindsaea nervosa*, pinnae from three different plants. B: *Lindsaea prolongata*. C: *Lindsaea rufa*, two leaves of juvenile plants (left) and two of adult plants (centre, right). D: *Lindsaea vieillardii*, juvenile and adult plant.

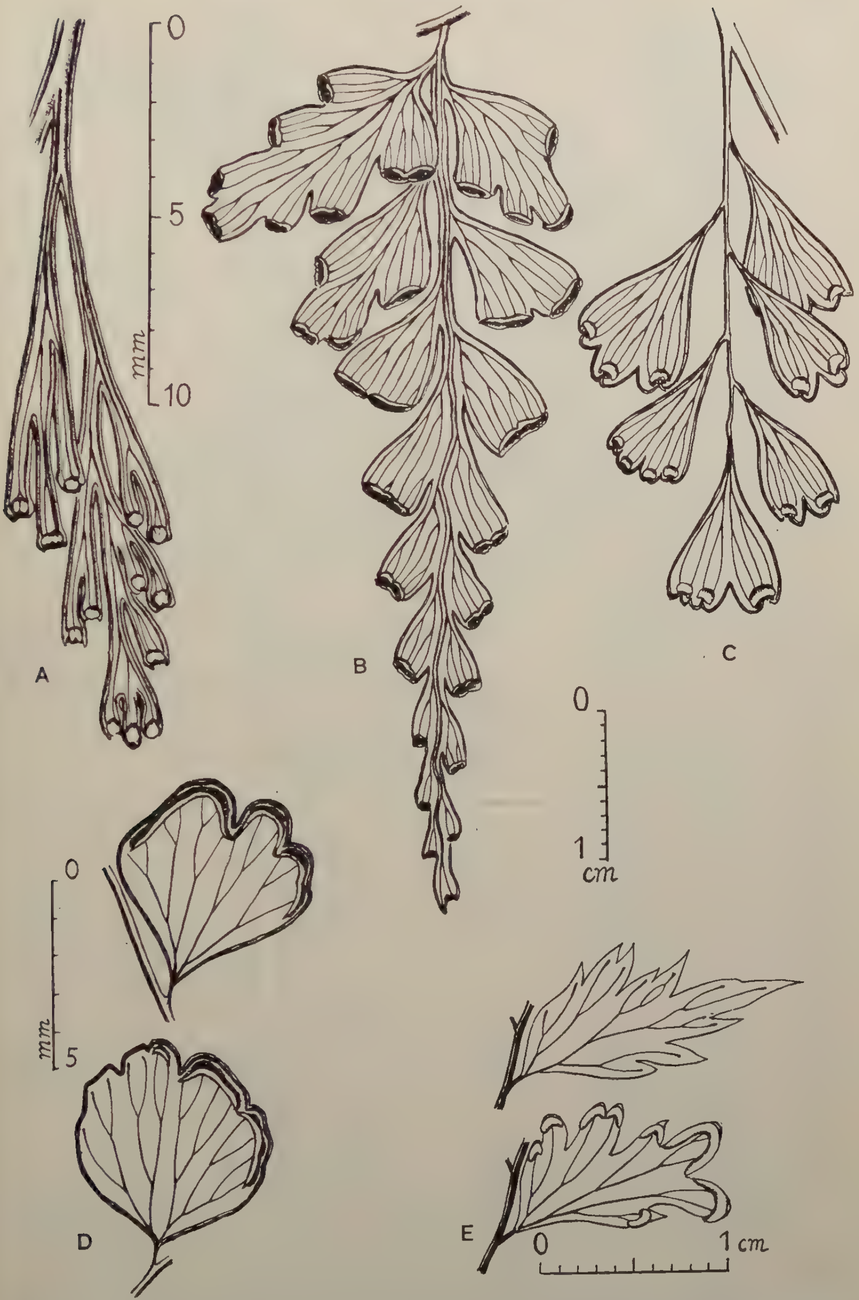

Fig. 3. A: *Sphenomeris angustifolia*, a pinnule. B: *Sphenomeris deltoidea*, a sec. pinna. C: *Sphenomeris alutacea*, a pinna. D: *Lindsaea rufa*, two pinnules. E: *Lindsaea prolongata*, a sterile and a fertile pinnule.

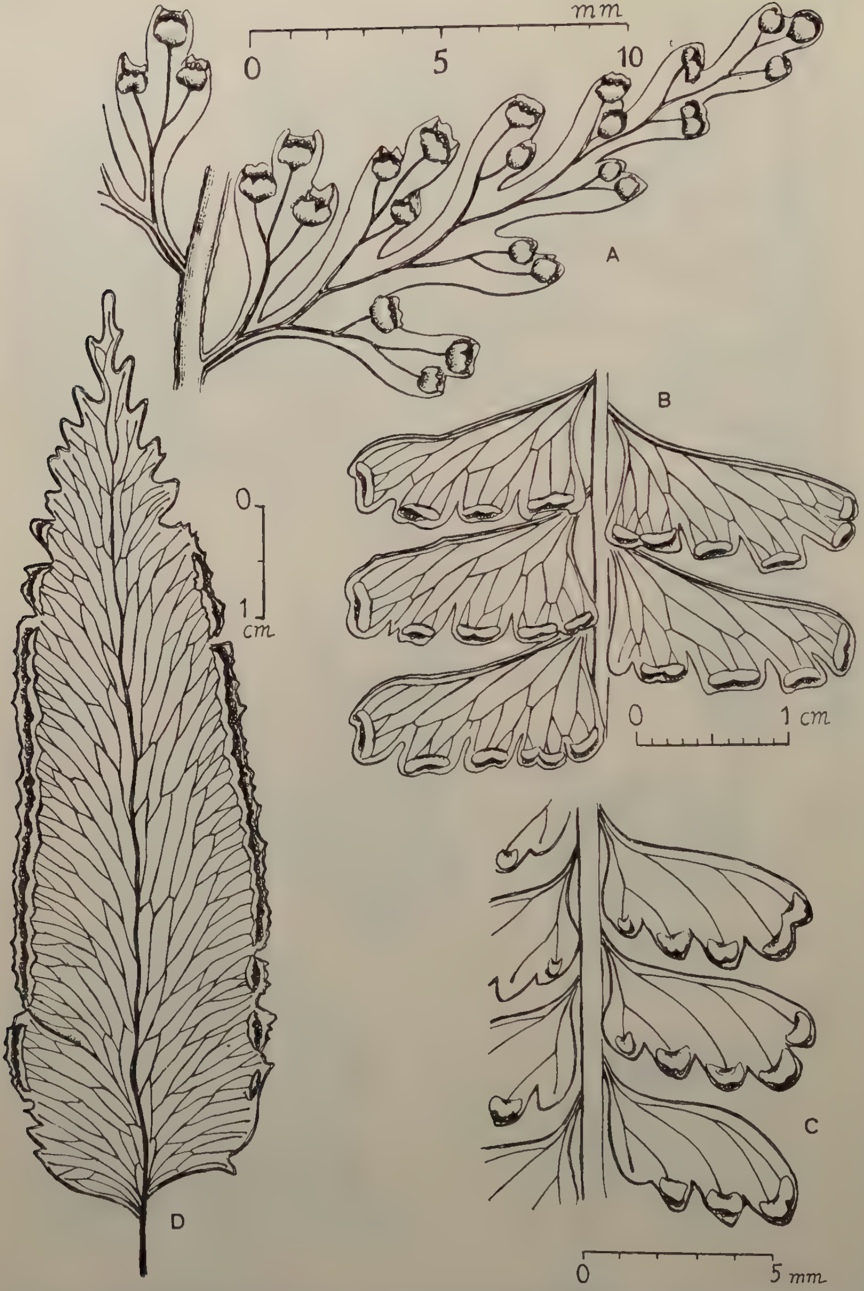

Fig. 4. A: *Lindsaea moorei*, an average upper pinna. B: *Lindsaea harveyi*, larger pinnules. C: *Lindsaea francii*, idem. D: *Lindsaea vieillardii*, a large pinna.

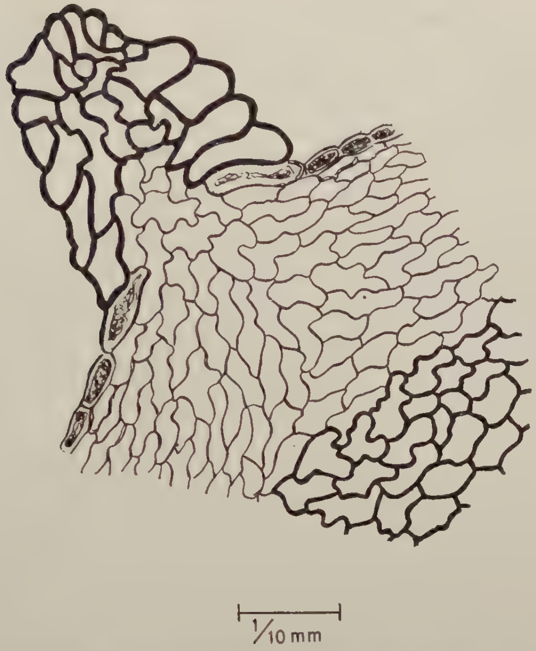

Fig. 5. *Lindsaea moorei* (McKee 5524), part of cross-section of rhizome showing insertion of scale.

sclerotic, stramineous, sometimes erose, entire to incised, the incisions few, usually 1 on the outer and 2 on the upper margin, rarely up to 2 mm deep; sterile pinnules regularly crenato-dentate. Veins elevated, pale, mostly twice forked, free. Sori continuous, or interrupted in incised pinnules, then often 4–6-nerval. Indusium pale, rigid, erose to subentire, ca. $\frac{1}{4}$–$\frac{1}{3}$ mm wide, not reaching the margin by an equal distance or less, reflexed at maturity. Spores pale brown, smooth, trilete, ca. 25 μ. **Fig. 2A**

Distribution: endemic.

Ecology: in rocky forests, in moist places, sometimes by watercourses, on ferritic and serpentine soil, 300–850 m. Apparently not rare.

Selected citations:

Franc '363' Koghi (MICH, US); id. '363', Mt. Dzumac (B, K, L, P); id. '1467', Mt. Dore (GH, Pic.-Ser.); id. '679', Baie du Sud (BRI, K, P); Vieillard '1540', Mt. Dore (P, type; isotype B); id. '1540' p.p., Wagap (B, L, P); Balansa 2694, Mt. Mou (B, BM, K, P, U); Däniker 322, Plaine des Lacs (Z); Sarasin 621, Yaté (P, Z); Buchholz 1260, Montagne des Sources (BISH); Compton 990, Mt. Nekando (BM); id. 791, Koghi (BM, type of *L. neocaledonica*); McKee 2617, Yaté Road (BM, GH, U).

The great variability in the shape of the pinnules of this species is mainly due to the influence of the degree of fertility.

4. **Lindsaea prolongata** Fournier, Ann. Sci. Nat. V. 18: 334, 1873. – *Schizoloma prolongatum* (Fournier) Kuhn, Chaetopt. 346, 1882; Brownlie, Pacific Science 15: 65, 1961, comb. superfl. – *Schizolegnia prolongata* (Fournier) Alston, Bol. Soc. Brot. 2a sér. 30: 24, 1956. – Lectotype: Balansa 1602. Mt. Arago (P!).
Lindsaea cheiroides Fournier, Ann. Sci. Nat. V. 18: 334, 1873. – Lectotype: Balansa 827, nr. La Conception (P!).

Rhizome short-creeping, 1½–2 mm in diam.; scales medium brown, narrowly triangular, to 2 mm long, with up to 5 rows of cells at the base, the apical part of one row comparatively short. Petioles close, dull, medium to dark brown, abaxially at least upward bi-angular, 15–40 cm long, 1½–2 × as long as the lamina, 1–1½ mm in diam. Lamina bipinnate or (in the basal pinnae) subtripinnate, herbaceous, mostly drying dark green, 10–20 cm long, to 15 cm wide, triangular-subpentagonal or in large leaves oblong, with 2–7 pinnae to a side and a ± conform terminal one; primary rachis similar to the upper part of the petiole, secondary rachises abaxially obtusely bi-angular or terete, reddish to dark, the dark colour ending in the cuneate bases of the pinnules. Pinnae patent or obliquely ascending, mostly long-acuminate, narrowly oblong to linear, the basal ones longest, the lower ones sometimes with a basal basiscopic pinnatifid or pinnate, prolongate secondary pinna. Pinnules in outline mostly obliquely elliptic, the larger ones 1¼–1½ × ¾–1 cm, unevenly pinnato-lobate (to ca. ⅓) on the upper and outer margin, the lobes acute and sometimes lobed again when sterile, rounded or narrowed-rounded when soriferous, then rarely lobed again; incisions in fertile pinnules up to 3 mm deep, sinuses acute, narrow to broad; some pinnules, especially the basal basiscopic ones, the upper ones, and the basal ones of the terminal pinna, sometimes prolongate-acuminate. Upper pinnules little reduced, none or a few connected with the pinna-apex which is linear-acuminate, serrate throughout or at the base hastato-lobate or pinnatifid, to 6 cm long, ⅔–1 cm broad; terminal pinna not rarely with the basal pinnules enlarged, more deeply lobed or even pinnatifid, forming a rudimentary transition from pinnate pinnae to lobed pinnules. Margin of pinnules often stramineous and sometimes sclerotic, often erose at the ends of the lobes. Veins evident, immersed or subprominulous, free, 2–3 × forked, pinnate and once or twice forked in the pinna-apices. Sori occupying the lobes but, except in shallow incisions, interrupted at the bottom of the sinus, on 1–6 vein-ends (entire and longer only in small pinnules), with very concave base, the receptacle laterally extending considerably beyond the vein-ends which bear it. Indusium pale, slightly erose to subentire, 0.3–0.4 mm wide, mostly not quite reaching the margin. Spores very pale brown, minutely tuberculate, trilete, ca. 22–26 μ. **Fig. 2B, 3E**

Distribution: endemic.

Ecology: in forests, 300–500 m.

Selected citations:

Franc '365', Koghi (B, BO, BRI, K, L, MICH, P, SING, U, US, Z); id. '365', St. Louis (B, BRI, US); Balansa 1602, Mt. Arago (P, type; isotype K); Vieillard 1540, Wagap (B, BM, GH, K, L, P, Pic.-Ser., U); Balansa 827, La Conception (P, type and isotype of *L. cheiroides*); Le Rat 565, Mt. Mou (B, K); McKee 4439, Koghi (BM, L, US); id. 4955, Thy Valley to Mt. Koghi (BM, US).

Brownlie (1961) showed that *L. prolongata* and *L. cheiroides* are conspecific and chose the former name for the combined species. His statement that *L. prolongata*, as understood by Fournier, does not have elongated terminal divisions is disproved by the material in the Paris herbarium, and also by the name chosen by Fournier. *L. prolongata* is closely related to *L. nervosa*; the combination of thin texture, peculiar terminal segments, and sori with very concave base occupying parts of the lateral edges of the lobes identifies it readily.

5. **Lindsaea ensifolia** Swartz, Schrad. Journ. 1800^{2}: 77 1801. – *Schizoloma ensifolium* (Swartz) J. Smith, Hooker's Jo. Bot. 3: 414, 1841. – *Schizolegnia ensifolia* (Swartz) Alston, Bol. Soc. Brot. 2a sér. 30: 24, 1956. – Type: unknown collector, Mauritius (S-PA!).
A description and the full synonymy of this well-known species will be given elsewhere, with the reasons why I cannot accept Domin's (1915) subdivision of this species. In New Caledonia there are two subspecies: ssp. *ensifolia* with scarcely or not abbreviated upper pinnae and a free, conform terminal one, and spp. *agatii*, with the upper pinnae gradually reduced and confluent with the basally lobed terminal segment. **Fig. 1C, D**

ssp. **ensifolia**

Distribution: tropical, here and there subtropical parts of the Old World, from West Africa to tropical Australia.

Ecology: open places, rocks, at lower elevation.

New Caledonian specimens seen:
Beaudouin s.n.s. loc. (K, P).

ssp. **agatii** (Brackenridge) Kramer, stat. nov.– Basionym: *Schizoloma agatii* Brackenridge, U.S. Expl. Exped. 16: 216, t. 30, f. 1, 1854. – Type: U.S. Expl. Exped. s.n. from Fiji (US? not seen; isotype K!).

Distribution: from Timor and New Guinea east to Samoa.

Ecology: like ssp. *ensifolia*.

Selected citations:

Vieillard 1557, Balade (B, K); Schlechter 14740, Yaouhé (B, BM, GH, HBG, K, L, Z); Franc '704', Plum (K, L, SING); id. '704', Baie du Sud (BRI, US); id. '704', Païta (BRI, Z); id. 704a, N'Go (K, L, P, SING); id. s.n. (Rosenstock-exs. 137), Baie des Pirogues (B, GH, L, MICH, US); McKee 2538, Hienghène (BM, K, U, US).

In some areas the two subspecies occur together, e.g. in Guam, New Guinea, tropical Australia, and New Caledonia. Intermediates are sometimes found there, notably in New Guinea and Australia. *L. ensifolia* ssp. *agatii* is often much like *L. heterophylla* Dryander; this is particularly true for a bipinnate form which occurs in New Guinea, Ponape, New Caledonia, and Australia; there are some subbipinnate intermediates. *L. heterophylla* has less regularly anastomosing veins, and the pinnules, notably the upper ones, are relatively wider. Its easternmost stations are in Borneo and the Philippines.

6. **Lindsaea vieillardii** Mettenius, Ann. Sci. Nat. IV. 15: 65, 1861. – *Schizoloma vieillardii* (Mett.) Kuhn, Chaetopt. 346, 1882. – *Schizolegnia vieillardii* (Mett.) Alston, Bol. Soc. Brot. 2a sér. 30: 24, 1956. – Type: Vieillard 1566, Balade (P!).
Lindsaea vieillardii Mett. var. *serrata* Compton, Jo. Linn. Soc. 45: 444, 1922. – Type: Compton 1765, Mt. Panié (BM!).

Rhizome rather short-creeping, 1½–2 mm in diam.; scales medium brown, almost acicular, to 1½ mm long, with up to 3 rows of cells at the base, about half of the scale of one row of cells only. Petioles rather close, atropurpureous to blackish, abaxially at least in the upper part bi-angular, ca. 10–25 cm long, exceeding the lamina, slender, ⅔–1 mm in diam. Rachis dark, the dark colour evanescing in the petiolules or occasionally in the basal part of the costae. Lamina herbaceous, drying dark green, simply pinnate, with 1–5 pairs of subopposite pinnae and a ± conform terminal one; pinnae petiolulate (to ca. 1 cm, the terminal one to 2 cm), or the upper ones subsessile; larger pinnae ligular, obtuse to acute, with obtuse or truncate base, up to 7 cm long and 2 cm wide, 3–7 × as long as wide; smaller pinnae and pinnae of young plants often ovate and much shorter. Lateral pinnae often upcurved and asymmetric; terminal pinna ± symmetric, rarely lobed at base. Costa approximately median, percurrent in the lower pinnae, slightly prominent beneath, mostly pale to base; veins immersed but evident, very oblique at the costa, arching to meet the margin nearly at right angles, the primary branches issuing from the costa at distances of about 5 mm, regularly reticulate, forming a series of low, long costal areoles and 1 or 2 partly overlapping series of progressively shorter ones or sometimes veins free from the costal areoles to the receptacle, in sterile pinnae their ends clavate and joined or free, ending well within the margin. Margin not thickened, grossly and very irregularly gashed, especially in sterile or incompletely fertile pinnae, with subobtuse, rather broad sinuses; completely fertile pinnae with an erose-sinuate or denticulate margin but nearly always with some deeper incisions as well (to 2 mm) that interrupt the sorus, these especially present toward the apex; teeth subacute or acute. Sori uniting several vein-ends, rarely all of a pinna, even around the apex, but mostly progressively more interrupted toward the apex of the pinna. Indusium ± sinuate, ca. 0.3 mm wide, strongly intramarginal, not reaching the margin by ca. 1 mm, ± reflexed at maturity. Spores pale brown, smooth, trilete, ca. 22–25 μ. **Fig. 4D**

Distribution: endemic.

Ecology: in shady forests, 350–800 m, apparently uncommon.

Selected citations:

Vieillard '1566', Balade (P, holotype; isotypes P, 5 sheets, B); id. '1566', Wagap (BM, GH, K, L, Pic.-Ser.); Franc 1367, Mt. Koghi (BO, BRI, K, L, MICH, Pic.-Ser., SING, US, Z); Schlechter 15042, Yaouhé (B, BM, GH, HBG, K, L, Z); Compton 1765, Mt. Panié (BM, type of var. *serrata*); Sarasin 313, Kanala (Z); McKee 5304, Chapeau Gendarme to Mt. Koghi (U).

Section *Paralindsaea* (Keyserling) C. Chr. (See KRAMER, 1957, p. 266).

7. **Lindsaea dimorpha** Bailey, Handb. Queensland Ferns 19, 1874, based on: *Lindsaea heterophylla* Prentice, Jo. Bot. 11: 295, 1873, non Dryander, 1797. – Type (not cited): Australia, without loc., Bailey s.n. (K!).
Lindsaea anogrammoides C. Christensen, Vierteljahrsschr. Naturf. Ges. Zürich 70: 223, 1925. – Type: Franc 1308, Conception (BM, herb. C. Christensen!).
Lindsaea minima Copeland, Univ. Calif. Publ. Bot. 14: 365, 1929, ex char. – Type Franc 2217, N. Cal., s. loc.? (MICH, not seen).

This rare species will be described in the account of the Australian species.

Distribution: n. e. Australia.

Ecology: one record 'cliffs 2000.' Apparently very rare in New Caledonia.

Specimen seen:

J. Roberts s.n., s.loc., Sept. 1886 (K).

BROWNLIE (1961) pointed out the identity of *L. dimorpha* and *L. anogrammoides*; Christensen (Ind. Fil. Suppl. III: 122, 1934) cited *L. minima* as a synonym of the last-named species.

8. **Lindsaea linearis** Swartz, Schrad. Journn. 1800²: 78, 1801. – *Adiantum lineare* (Swartz) Poiret, Encycl. Suppl. I: 139, 1810. – Type: presumably from Australia (not stated; not seen).

A description of this well-known species, common in Australia and parts of New Zealand, will be given elsewhere, with the full synonymy.

Ecology: open places, on ferritic and serpentine soil, ca. 600–1000 m; data few. Apparently very localized in New Caledonia.

Specimens seen:

Deplanche s.n., Mt. Mou (K); id. 140, Mt. Mu (= Mou?) (B); Däniker 817, 817a, Mt. Mou (Z); Franc 1309, ibid. (BRI, K, P); Pancher s.n., ibid. (P); Balansa 2735, ibid. (P); id. 57, near Nouméa (P); Schlechter 14754, Yaouhé (B, HBG, K, P); Vieillard 1556, Fort de France (P); Le Rat 81, Mt. Mou (P).

Section *Temnolindsaea* Kramer, Acta Bot. Neerl. 6: 176, 1957. This section, described for neotropical species, by definition comprises a small group of Old World, mainly Malesian, species. It is, however, quite possible that these are more closely related to the section *Synaphlebium* than to the American species.

9. **Lindsaea francii** Rosenstock, Fedde Rep. 9: 73, 1910. – Type: Franc 1420, Mt. Tao (P!).

The following description is confined to the main features and the points omitted or incorrectly described by Rosenstock.

Rhizome short-creeping, knotted, 3–5 mm thick; scales dark brown, narrowly triangular, to 2 mm (or more?) long, with up to ca. 7 rows of cells at the base. Petioles clustered, stramineous to pale brown, smooth, quadrangular and quadrisulcate, ca. 2 mm thick, to 50 cm long, exceeding the lamina. Lamina bipinnate, oblong; rachis abaxially bi-angular, sulcate. Pinnae spreading or somewhat ascending, 12–15 to a side and a conform terminal one; upper and lower pinnae slightly shortened, the middle ones ca. 12 cm long, 12 mm wide, linear, acuminate; secondary rachises abaxially bi-angular, scarcely sulcate. Pinnules herbaceous, closely and regularly set, 40–50 to a side, the basal ones slightly, the upper ones strongly reduced and confluent into a pinnatifid pinna-apex; larger pinnules asymmetrically ovate, 6 × 2½ mm, the upper margin with 3, the outer with 1 incision, the incisions oblique, up to ca. 1 mm; lobes mostly subacute or acute. Veins immersed, evident, one running to each lobe. Sori uni- or occasionally the outer one binerval; receptacle on the same level as the sinus; indusium pale, subentire or gashed, often with concave base, not reaching the margin by less than its width but often the sides of the lobes, ½ mm wide. Spores very pale, smooth, trilete, ca. 22 μ. **Fig. 4C**

Distribution: only known from type collection (see above; holotype P, isotypes P, 2 sheets; U; fragm. US).

Ecology: in forest, clay soil, 600 m.

Rosenstock (l.c.) compared this species with *L. davallioides* Bl. and *Davallia* (*Lindsaea*) *delicatula* Christ, particularly with the latter. It is not closely related to either one but resembles most closely *L. kingii* Copeland, described a year after *L. francii*.

Section *Synaphlebium* (J. Smith) Diels in Engler und Prantl, Nat. Pfl. I^4: 221, 1902. – *Synaphlebium* J. Smith, Jo. Bot. 3: 415, 1841, as genus.

10. **Lindsaea harveyi** Carruthers ex Seemann, Fl. Vit. 338, 1873. – *L. decomposita* auctt. plur. poster., non Willd.; *L. cultrata* auct. non (Willd.) Swartz; Fournier, l.c., p. 333; *L. gracilis* auct. non Blume; Fournier, l.c., p. 333. – Lectotype: Harvey s.n., Fiji (K!).

Recent authors, e.g. COPELAND (1929a), included *L. harveyi* in *L. decomposita* Willd. This species which must be properly called *L. cultrata* (Willd.) Swartz has usually been construed far too widely; it occurs almost exclusively in Malesia. *L. harveyi* is much closer to *L. obtusa* J. Smith in Hooker, another chiefly Malesian species that is usually included in *L.* '*decomposita*'. *L. harveyi* and *L. obtusa* can sometimes be distinguished only with difficulty, especially juvenile and depauperate plants; they should perhaps be treated as subspecies. A description will be given in the account of the species of the smaller Pacific islands. The New Caledonian specimens are nearly all simply pinnate and apparently much less well developed than most collections from Melanesia and Polynesia. This makes the identification less certain, as in the section *Synaphlebium* generally incomplete or depauperate specimens often cannot be named with certainty. **Fig. 4B**

Distribution: Solomon Islands to Samoa and Tonga.
Ecology: in forests, by streams, 100–400 m; very few data.

Selected citations:

Franc 1432, Mt. Tao (P, S-PA); Vieillard '1553', Wagap (B, L, P, Pic.-Ser.); id. '1553', Balade (P, U); Balansa 1601, Baie St. Louis nr. Nouméa (P); Cribs 1057, Forêt de Bâ (K, P).

EXCLUDED SPECIES

Lindsaea cultrata Swartz. – See note under *L. harveyi* Carr. ex Seem.

Lindsaea gracilis Blume. – Idem.

Lindsaea heterophylla Dryander. – See under *L. ensifolia* Swartz and *L. rufa* Kramer.

Lindsaea microphylla Swartz. – FOURNIER (1873), p. 336, cited a specimen he had not seen from New Caledonia. There is one in the Paris herbarium marked 'in Nova Caledonia leg. Ch. Vieillard et Plancher' . . . Cl. Lenormand donavit 1857.' The species has never again been found there, and its occurrence, though certainly not impossible considering the presence of other Australian species, is at present very doubtful.

Lindsaea tetragona Kramer. – A specimen belonging to this species, to be described shortly, in the Kew herbarium is marked 'New Caledonia, Macleay.' The species extends to Tahiti but has never been re-collected in New Caledonia, nor in the New Hebrides.

Sphenomeris retusa (Cav.) Maxon. – The specimens cited by FOURNIER (1873), p. 337 (as *Lindsaea retusa* Mett.) belong to *Sphenomeris chinensis*. A specimen in the Paris herbarium collected by Labillardière is *Sph. retusa*, but its occurrence in New Caledonia seems doubtful as there are no later collections.

Tapeinidium denhamii (Hooker) C. Chr. – Strange s.n. (K) is labelled 'New Caledonia' and a collection without further data (B, K) 'Isle of Pines'. I suppose the plants came from the New Hebrides or other parts of Melanesia.

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FOLIAR SCLEREIDS IN THE MARCGRAVIACEAE

A. C. DE ROON

(*Botanical Museum and Herbarium, Utrecht*)

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Abstract

A survey is given of the types of the sclereids and the sclereid patterns occurring in the leaves of the Marcgraviaceae. Eight main categories of sclereids are distinguished on the base of the morphology of the sclereids. A comparison is made with the foliar sclereids found in some other families. The systematic value and the function of the sclereids are briefly discussed. Some new combinations of names are published.

Introduction

'Sclerenchymatic idioblasts', i.e. the kind of cells which are usually indicated by the name 'sclereids', are very common in the *Marcgraviaceae*. They are found in a great diversity of forms and often in large numbers in various parts of the plants, viz. in the cortex and the medulla of the shoots, in the leaves, in the nectaries and in the perianth, the pistil and the pericarp. In this paper we will confine ourselves mainly to the foliar sclereids.

The presence of idioblastic sclereids in leaves and other parts is a phenomenon found in species belonging to many different families. In the works of Solereder (1899) and of Metcalf and Chalk (1950) a large number of examples are to be found. Also a large amount of data are given in papers published in various periodicals. For surveys we can refer to Foster (1944, 1949), Rao (1951a, 1957b), for the older literature moreover to Wijnaendts Francken (1890) and for sclereids occurring in conifers to Sterling (1947) and to Al-Talib and Torrey (1961).

In recent studies on sclereids attention is drawn in particular to three aspects of this subject, namely the morphology, the ontogeny and the taxonomic value. For several purposes a practical classification of the sclereids based on their morphology can be of use. However in view of the enormous variability found among the sclereids, it seems advisable to name only the main categories. And as the distinguishable types are almost always connected to each other by intermediate forms, it will often be necessary to add a qualifying description. It seems to me that this is preferable to the elaboration of a classification which aims at completeness but would lose a good deal of its usefulness. A natural classification of the sclereids can not be based on their morphology alone, therefore other characters such as the structure and the ontogeny must be considered (cf. Foster, 1949; Rao, 1951a, 1957b). The great diversity in form shown by the sclereids has led to a chaotic terminology (cf. Foster, 1944) and to avoid a further increase of this chaos we have confined ourselves, where possible, to the general terminology used by Tschirch (1889) and Foster (1949) and to the terminology used by Richter (1916, 1917, 1920) for the sclereids found in the *Marcgraviaceae*.

The first one who set up a classification of sclereids was Tschirch (1889). He distinguished four main categories of sclereids, viz. 'brachysclereids', 'macrosclereids', 'osteosclereids' and 'astrosclereids'. As clearly appears from the examples given by him, he used these terms in a very broad sense, broader than most of the authors after him did. A classification of foliar sclereids is made by Rao (1951a, 1957b) who distinguishes as form types: 'spheroidal sclereids', 'osteosclereids', 'fusiform sclereids', 'filiform sclereids', 'astrosclereids' and 'crystalliferous sclereids', which are classified in three main groups on the basis of their ontogeny. The general morphological classification of Tschirch (1889) proves still to be usable though a certain modification is necessary. So it might be advisable to treat the non-idioblastic, tissue-forming sclerenchyma cells as a separate category along with the categories of the idioblastic sclereids and the fibers.

In the studies on the ontogeny of foliar sclereids two problems had special attention, the origin of the sclereid initials with their possible relation to the terminations of the veinlets and the method of growth of the cells. Foster (1946, 1947) discovered that beside a random distribution, foliar sclereids can be restricted to the ends of the veinlets. In several genera such terminal sclereids are a common phenomenon. In the *Marcgraviaceae* the foliar sclereids are transformed palisade or spongy parenchyma cells; their distribution is diffuse and there is no evidence for an ontogenetic relation with the vascular bundles. However, as no ontogenetic investigations are made, these and other remarks in this paper regarding the origin of the sclereids are only based on the form and the position of the sclereids and must therefore be taken with some reservation. The necessity for this caution is illustrated by the following examples: the osteosclereids found in the leaves of *Mouriria huberi* Cogn. (Foster, 1947), which connect the upper with the lower epidermis like pillars, develop from initials found in the spongy parenchyma region at the terminus of the procambial strands and the similar type of sclereids found in the leaves of *Olea dioica* Roxb. (Rao and Kulkarny, 1952) represent transformed palisade cells. The Marcgraviaceous 'palosclereids' very probably are transformed palisade parenchyma cells but a similar type of sclereids occurring in the palisade layer of the leaves of *Diospyros discolor* develop from initials situated in the spongy mesophyll (Rao, 1951c).

Determination of sclereid initiation has become subject to experimental manipulation (Foard, 1958, 1959; Al-Talib and Torrey, 1961). Al-Talib and Torrey concluded from their experiments that the determination of sclereid initials in foliar leaves of *Pseudosuga menziesii* is clearly under some precise control of changing physiological conditions active during leaf and shoot development. Insofar as there is evidence on the matter, it would seem probable that hormonal factors, especially auxins, may play a role in determining when and where sclereid initials will develop. Their experiments suggest that auxin levels in the leaf influence the development of sclereids, with high auxin levels tending to suppress sclereid development. I think that for the taxonomist these experiments are of great interest and importance as will be discussed in the chapter on the taxonomic value of sclereids.

In the present article the results of a study of the foliar idioblastic sclereids of the *Marcgraviaceae* are presented. This study covered the form and the classification of the sclereids, their distribution and their arrangement into patterns. A comparison is made with the foliar sclereids of some other families. The value of sclereids as a taxonomic character is discussed. Some remarks are made on the possible function of foliar sclereids.

MATERIAL AND METHODS

The investigations are based on the study of leaves of herbarium specimens of a great number of species. The sclereids were studied in cleared leaf sectors, in hand sections and after isolation from macerations. The leaves were cleared following the technique of FOSTER (1946, 1949) and mostly stained with saffranine. Macerations were made by one of the usual methods.

As it is intended to give in this paper a general survey only, and no detailed studies on the sclereid patterns of the individual species, no list of all the specimens studied is given but the specimens sclereids of which are figured are mentioned in the explanation of the figures.

NEW COMBINATIONS

For a correct citation of some species it is necessary to publish here some new combinations of names, anticipating a monographic treatment of the family which is in preparation. This regards the following species:

Souroubea bicolor (Bentham) de Roon comb. nov.
Basionym: *Ruyschia bicolor* Bentham, Bot. Voy. Sulph.: 73, t. 29. 1844.

Souroubea loczyi (Al. Richter) de Roon comb. nov.
Basionym: *Norantea loczyi* Al. Richter in Math. u. Naturw. Berichte aus Ungarn 31: 115. 1920.
Synonym: *Souroubea triandra* Lundell in Phytologia 1: 244. 1937.

Souroubea platyadenia (Gilg) de Roon comb. nov.
Basionym: *Ruyschia platyadenia* Gilg in Engler, Bot. Jahrb. 25, Beibl. 60: 34. 1898.

Norantea brachystachya (Rusby) de Roon comb. nov.
Basionym: *Souroubea brachystachya* Rusby in Bull. N.Y. Bot. Garden 8: 103. 1912.

Norantea jimenezii (Standley) de Roon comb. nov.
Basionym: *Ruyschia jimenezii* Standley in Field Mus. Bot. 18: 699. 1937.

Marcgravia goudotiana (Triana et Planchon) de Roon stat. nov.
Basionym: *Marcgravia rectiflora* Triana et Planchon var. goudotiana Triana et Planchon in Ann. Sc. Nat. ser. 4, 17: 366. 1862.

Marcgravia leticiana (Macbride) de Roon stat. nov.
Basionym: *Marcgravia flagellaris* Poeppig ex Wittmack var. *leticiana* Macbride in Candollea 5: 387. 1937.
Synonym: *Marcgravia trinitatis* Presl var. *leticiana* Macbride in Field Mus. Bot. 13A, 2: 707. 1956.

SURVEY OF THE TYPES OF SCLEREIDS FOUND IN THE MARCGRAVIACEAE

Among the foliar sclereids of the *Marcgraviaceae* a high degree of diversity is found. On the base of their form they may be arranged in eight main categories, three of which were already distinguished by TSCHIRCH, viz.: 'brachysclereids', 'astrosclereids' and 'osteosclereids', completed with five categories distinguished by RICHTER, viz.; 'ophiurosclereids', 'librosclereids', 'palosclereids', 'rhizosclereids' and 'idiosclereids'.

The wall of the sclereids may be thickened to a varying degree and it often shows a distinct lamellation which becomes still more clearly visible in polarised light. The outside of the sclereids is usually smooth, spicules as were found by FOSTER (1944) on the sclereids of *Camellia japonica*, were never met with. Pits may be present in all the various types. In the sclereids provided with long projections pits are only found in the 'central body'.

The simplest type among sclereids is that found in the '*brachysclereids*' or 'stone cells'. Sometimes they are no larger than the surrounding parenchyma cells, but often they exceed these in size considerably. Two forms of brachysclereids are found in the *Marcgraviaceae*. Brachysclereids with a rather thin wall and a wide lumen are found in the spongy parenchyma in the leaves of several species, mostly in small numbers only and sometimes united into small clusters. Brachysclereids with very thick and conspicuously lamellated and pitted walls are frequently found in various parts e.g. the cortex and the pith of the shooth, the sepals and the pericarp; they are often united into clusters. In the corolla of the *Marcgravia* species they form a hard solid layer. In the leaves they are sometimes crowded around the hypophyllous glands and immediately below the midrib they may be numerous too; here transitions between them and macrosclereids and astrosclereids are frequently met with. In wound tissue and other abnormal cork developments brachysclereids are often seen as well; mostly they have the same form as the cork cells; RICHTER (1917) speaks in this case of '*phellosclereids*'.

The final form of a sclereid depends greatly upon the tissue in which it develops, particularly on the shape of the cells out of which such a tissue is formed. So in the palisade parenchyma of part of the *Norantea* and *Souroubea* species sclereids are found which agree in shape with the surrounding parenchyma cells. They are sometimes arranged in clusters or rows but mostly they are isolated. The thickening of their walls varies from slight to very strong, and the width of the cell lumen, accordingly, from wide to narrow; the pits in the walls are very conspicuous (Plate I, Figs. 1–3). In the classification of TSCHIRCH these rod-shaped 'palisadic sclereids' belong to the category of the macrosclereids. TSCHIRCH used the term macrosclereid for the columnar non-idioblastic sclereids which form a palisade layer in the testa of many Papilionaceae, as well as for idioblastic foliar and cortical sclereids (TSCHIRCH, 1889, fig. 347). In my opinion it would be better to keep the non-idioblastic, tissue-forming sclereids out of a classification of idioblastic sclereids, and to use the term 'malpighian cells' for the above mentioned sclerenchyma cells of seed coats.

Richter proposed the term '*palosclereids*' for the sclereids of the palisade parenchyma described above, which term is adopted in the present article, and by which therefore is meant macrosclereids situated in the palisade parenchyma, whether they have retained the shape and the size of the parenchyma cells or not.

A special form of palosclereids is found in *Norantea spiciflora* and in various species of *Souroubea*, e.g. *S. crassipes*, *S. pachyphylla*, *S. didyma*, *S. bicolor* and *S. vallicola*. They are of the same height as the surrounding palisade cells, but their diameter is larger to very much larger than that of these cells. In transverse sections they are usually rectangular. They often form rows running in the direction from the base to the top. The walls are often but slightly thickened and they are therefore not always easily recognisable as sclereids. In *Norantea spiciflora* and *Souroubea vallicola*, and occasionally also in some other species, the walls are more strongly thickened, and in that case the pits and the lamellated structure of the wall are quite conspicuous (Plate I, Fig. 7; Plate II, Figs. 2, 3). In the above mentioned *Souroubea* species, in which the palisade parenchyma consists of two layers, the palosclereids are always found in the layer adjoining the epidermis.

Palosclereids provided with short protrusions and showing therefore a development in the direction of the rhizosclereids which will be discussed below, have been found in *Norantea cuneifolia* and in *N. spec.*, Cuatrecasas 16618 (Plate I, Figs. 1, 2).

The '*rhizosclereids*' or 'rooting sclereids' consist of a central part comparable in form to a palosclereid and occupying a similar position between the palisade cells, a number of root-like protrusions extending into or on top of the spongy parenchyma, and often also some, usually shorter, processes extending between the epidermis and the top of the palisade cells. The processes at the upper end may differ considerably in length; occasionally they extend into the longitudinal direction of the leaf (Plate VI, Figs. 4–7). Sometimes they are bent downwards at the end, and then the hooklike top penetrates between the palisade cells (plate V, Fig. 8).

Within the category of the rhizosclereids three types are distinguished in the *Marcgraviaceae*. In the first type the projections at the lower end of the central part extend into the direction of the lower epidermis, and they are mostly somewhat spreading (e.g. Plate III, Figs. 9–13; Plate IV, Figs. 4–6; Plate V, Figs. 6–10; Plate VI, Figs. 10–14). In the second type the projections may all or in part extend in a longitudinal direction on the top of the spongy parenchyma (Plate VI, Figs. 20, 21, 23). In the most deviating type the central part is shortened and more or less contracted in the middle, hour-glass-shaped, and the protrusions at the top as well as at the base are long and extending in the longitudinal direction; the number of them, as well at the top as at the base, is moreover reduced to two to four (Plate VI, Fig. 22).

Rhizosclereids are found in *Ruyschia* and *Souroubea* (type 1) and in *Norantea* subgen. *Marcgraviastrum* (type 1, 2, and 3). In some *Marcgravia* species sclereids are met with which extend partly into the palisade parenchyma, but they are of another type than the rhizosclereids described above. They will be described in detail further on.

In the spongy parenchyma the sclereids show a much greater diversity; they are, moreover, much less regular in form. In the first place we will mention here the large group of the '*astrosclereids*', in which all sclereids are included with an irregular shape caused by the presence of ramifications or of shorter or longer projections or arms. This is a very heterogenous assemblage, so that the term can be used only in a rather vaguely descriptive way. The many kinds of astrosclereids which are encountered in the *Marcgraviaceae*, may be arranged in a few series, the members of which gradually pass from the star-shaped form of the typical astrosclereid into more specialized types like the ophiurosclereids, the librosclereids and the idiosclereids.

In the typical form of astrosclereids met with in the *Marcgraviaceae* there is a central part provided with a less strongly to very strongly thickened wall and an usually rather small to very small cell lumen and with a number of projections extending in all directions and rather short, their length not exceeding more than a few times the diameter of the central part (Plate IV, Figs. 7–12; Plate V, Figs, 11, 12, 14; Plate VI, Fig. 15). This type of astrosclereids is connected by transitions with the brachysclereids. They occur in the spongy parenchyma of the majority of the species belonging to the genus *Ruyschia* and in a fair number of the species belonging to other genera. They are not confined to the leaves but occur also in other parts, so e.g. in the cortex of the shoots, in the pedicels, sepals, etc., and they are often present in large numbers and often crowded.

In some astrosclereids of this type there is a tendency towards reduction of the size of the central part and towards an increase in length of the projections. If this tendency becomes more pronounced the astrosclereids pass into the type for which Richter used the name '*ophiurosclereids*'. The latter possess a relatively small central part and are provided with very long projections, i.e. that the length of these arms exceeds the diameter of the central part many times; the arms are situated, as a rule, in a plane which runs parallel to the surface of the leaf (Plate III, Figs. 14–16; Plate IV, Figs. 14, 18–23; Plate V, Figs. 13, 23, 24, 27). This type of sclereid is included by Tschirch in his category of the astrosclereids. Richter used the name ophiurosclereids for the very same type of sclereids as Jönsson (1880), who introduced this term in his study of the leaf anatomy of the *Proteaceae*.

Often ophiurosclereids are met with in which some of the arms are very strongly elongated, whereas the other projections are much shorter; in this case the elongated arms extend in opposite directions (e.g. Plate III, Figs. 16–18; Plate V, Fig. 22).

If the number of the elongated arms is reduced to four, three or two, we arrive at a type for which Richter introduced the name '*librosclereids*' or 'fibre-shaped sclereids'. The typical librosclereids are provided with a very small central part and two very long arms extending in opposite directions and occasionally accompanied by a few extremely small projections; this type therefore shows a striking resemblance to a fibre (Plate II, Fig. 10; Plate III, Figs. 26–28; Plate IV, Fig. 25; Plate V, Figs. 25, 28; Plate VI, Figs. 28–37). They may reach a considerable length; in *Norantea spec.*, Killip and Cuatrecasas 39159 for instance, they are circa 6 mm long. A type with usually four arms, and therefore more or less H-shaped is also often encountered (Plate III, Figs. 22–25; Plate V, Fig. 26; Plate VI, Figs. 31, 34). This type of sclerenchyma cell is also indicated as 'poil interne en H' by Van Tieghem (1866, 1891), as 'trichoblast' by Sachs (1874) and as 'trichosclereid' by Bloch (1946). Librosclereids in the leaf are always oriented lengthwise, i.e. parallel to the midrib.

Large ophiurosclereids and librosclereids with slender arms are found, all or not in combination, in *Ruyschia phylladenia*, several *Souroubea* species, e.g. *S. guianensis*, *S. corallina*, *S. bicolor* and *S. sympetala*, and most of the *Norantea* species belonging to the subgenus *Marcgraviastrum*.

Ophiurosclereids and librosclereids, especially the H-shaped ones, are often found in the cortex and occasionally also in the medulla of young shoots; in the peduncle and in the axis of the inflorescence and in the pedicels they may also be present. In some species of *Souroubea* and of *Marcgravia* and in the subgenus *Marcgraviastrum* of *Norantea* they are a conspicuous feature of these parts.

A category of sclereids for which Richter proposed the name '*idiosclereids*' is met with in a fairly large number of *Marcgravia* species but outside this genus only in *Norantea spiciflora* and *N. jimenezii*. The sclereids of this category are very polymorphic and very variable in shape and size. Some types can be distinguished by the structure of the wall and the ramification of the cell (Plate I, Fig. 8; Plates VII-X). In the classification of Tschirch these sclereids belong to the category of the astrosclereids but in my opinion it is better to treat the idiosclereids as a distinct category and to assign to the astrosclereids only the more or less pure stellate forms. Rao (1950b) named similar types of sclereids of the leaves of the Proteacea *Leucospermum hypophyllum* R. Br. 'polymorphic sclereids'.

Finally there is the category of the '*osteosclereids*', columnar sclereids with mostly dilatated, lobed or ramified ends, to which Tschirch (1889) assigns both tissue forming sclereids from seed coats and idioblastic foliar sclereids. Osteosclereids are known from the leaves of a few *Marcgravia* species where they connect the upper and the lower epidermis like pillars, e.g. in *M. brownei*, *M. goudotiana* and *M. schippii* (Plate XII).

Below the midrib the sclereids often show a deviating form; these sclereids have been left out of consideration in the survey given above. Near the margin of the leaf usually but few or hardly any sclereids are seen, though occasionally some large brachysclereids or macrosclereids are found here (Plate II, Figs. 4, 8). Another noteworthy feature is that in some species some of the cells of the spongy parenchyma, occasionally even a large part of them, possess a thickened wall with remarkable large pits (Plate I, Fig. 4).

The various types of sclereids can be placed in morphological series which show the relations among the types and their possible derivation. For the sclereids which occur in the genera *Norantea*, *Ruyschia* and *Souroubea* this is shown on Plate XIII.

In the genus *Marcgravia* the sclereids deviate in their form, as a rule, rather strongly from those occurring in the other genera. The delimitation of the various types is more difficult, and within the categories the diversity is mostly larger. Palosclereids and rhizosclereids are entirely lacking in the genus, whereas the astrosclereids, the ophiurosclereids and the librosclereids are represented by forms which deviate from those found in the other genera. The idiosclereids are found in the genus in an enormous variability.

Brachysclereids like those of *M. soropaniana*, and two other species figured on Plate VII (Figs. 1–3, 7), may be regarded as representing the basic form from which the others can be derived. By way of the intermediate idiosclereidlike forms provided with a larger number of protrusions and with a wide cell lumen found in *M. gentlei* (Fig. 8), *M. williamsii* (Fig. 9) and *M. coriacea* (Figs. 13, 14) we arrive at the large and long idiosclereids provided with a rather wide cell lumen found e.g. *M. spec.*, Killip and Cuatrecasas 39100, (Fig. 15), *M. lineolata* (Figs. 18, 19) and *M. evenia* (Fig. 17), whereas by the way of the sclereids of *M. mexicana* (Plate VIII, Figs. 6, 8, 9) we come to the elongated, unbranched or but slightly branched idiosclereids of *M. angustifolia* (Figs. 1, 2), *M. magnibracteata* (Figs. 4, 5), *M. crenata* (Fig. 2), and the more branched sclereids like those of *M. comosa* (Figs. 7, 10, 12). In *M. spec.*, Skutch 3762 (Plate IX, Fig. 1), *M. macrophylla* (Figs. 2, 3), *M. rectiflora* (Figs. 4, 5), *M. oblongifolia* (Figs. 8–13) and *M. flagellaris* (Fig. 14) we note a gradual increase in the number of projections and in their length, leading to an irregular, often very disorderly form.

All the sclereids figured on Plate IX are shown as they appear to us in a transverse section of the leaf. With the exception of the one shown in Fig. 14 they are all oriented perpendicular to the surface of the leaf. The longer projections are usually oriented parallel to the surface.

Starting from these forms there seems to be a differentiation in two directions. The central part may grow out perpendicular to the surface of the leaf with the result that either its upper end or one or more of the protrusions reach the upper epidermis. This kind of differentiation is shown by the forms figured on Plate X. A portion of the central part and occasionally some of the projections penetrate in this case between the palisade cells, and, due to this, these sclereids remind us more or less of rhizosclereids. However, it does not seem probable that they developed out of cells belonging to the palisade tissue, as they ought to have done if they really were rhizosclereids. The end of these sclereids which abuts on the epidermis is often more or less flattened, and the extension of the projections more or less parallel to the surface of the leaf is sometimes quite considerable (Plate X, Fig. 9), but this is not always so. On Plate XII a number of forms are figured in which the elongation perpendicular to the surface of the leaf has proceeded so far that these sclereids form a kind of pillars resting on the lower epidermis and bearing the upper one. In *M. goudotiana* (Figs. 2, 3) these osteosclereids still possess some lateral projections, but in the other forms which are shown on this plate, these lateral projections are completely lacking. These osteosclereids may perhaps be derived from idiosclereids like those which are found in the leaves of *M. magnibracteata* (Plate VIII, Fig. 5), but the affinity with a type like that found in *M. spec.*, Cowan 38207 (Plate X, Fig. 1) is probably more pronounced.

A differentiation in the other direction is found in the forms shown in the Figures 6–14 of Plate IX. These sclereids too are oriented with the central part more or less perpendicular to the surface of the leaf, but they show an ever increasing expansion in the direction parallel to the surface. Fig. 14 shows a transition towards the large astro- and ophiurosclereids shown on Plate XI. These kinds of sclereids (Plate XI) are usually somewhat coarser and less regular in shape, and are often provided with a larger number of projections directed towards the surface of the leaf as compared to the ophiurosclereids occurring in the genera *Norantea* and *Souroubea*.

FOLIAR SCLEREID PATTERNS

For the characterisation of the species it is not only the form of the sclereids which is of importance but also their frequency, varying from scattered to densely crowded, their orientation in the leaf, e.g. perpendicular to the epidermis or parallel with the latter, and the occurrence of one type or a combination of different types of sclereids in the leaf, in brief all the characters which together constitute the 'sclereid pattern'.

The following descriptions of sclereid patterns must be regarded with some reserve, since often only a few leaves or even just one leaf could be studied. A thorough study of the variation of the sclereid pattern in the leaves of the individual and within the species is desirable but could be made here only in a few species. In these species the sclereid pattern appears to be rather constant, though a certain variation exists possibly related to ecological factors. This problem will be discussed elsewhere in this paper.

Striking distributional patterns with a concentration of sclereids in a certain zone of the leaf as are e.g. found by FOARD (1959) in the leaves of *Camellia japonica* or by KITAMURA (1956) in the leaves of *Sciadopitys verticillata* are not met with in the *Marcgraviaceae*. The midrib region and the outmost marginal zone, however, are different from the rest of the leaf and must let out of consideration.

In the leaves of all *Ruyschia* species which could be investigated, with the sole exception of those of *R. phylladenia*, large numbers of rhizosclereids (type 1) are inserted between the palisade cells, whereas in the spongy parenchyma many coarse and thickwalled astrosclereids and occasionally transitions between the latter and ophiurosclereids are met with. *R. phylladenia*, however, occupies a particular position in the genus in this respect, for in the leaves of this species slender rhizosclereids with usually long projections extending into the spongy parenchyma, and most of them also with long projections below the epidermis are found, whereas in the spongy parenchyma a large number of ophiurosclereids and of librosclereids are found.

On account of the characters shown by the sclereids the species of the genus *Souroubea* may be divided into three groups which appear to differ also in other morphological features. The first group, which comprises the species *S. dasystachya*, *S. exauriculata*, *S. gilgii*, *S. loczyi*, *S. platyadenia* and *S. venosa*, is characterized by the scarcity or complete absence of sclereids in the leaves. However in *S. gilgii*, and occasionally also in *S. exauriculata*, the sclereids are found to be somewhat more numerous; in this two species some palosclereids and, in the spongy parenchyma, also brachysclereids are found, the latter are mostly confined to the vicinity of the midrib, though in *S. gilgii* they are also found occasionally in other parts of the leaf. In *S. gilgii* the diversity in form is also greater than in the other species; in the vicinity of the leaf margin some large brachysclereids are found (Plate II, Fig. 8), and elsewhere transitions are seen from brachysclereids by the way of ophiurosclereids to librosclereids; librosclereids themselves are also present; none of these types, however, is found in large numbers (Plate II, Fig. 10).

In the second group of species which may be distinguished in the genus *Souroubea*, and which comprises the species *S. bicolor*, *S. crassipes*, *S. didyma*, *S. pachyphylla*, *S. vallicola* and *S. spec.*, Bang 2401, the palisade parenchyma, which in this group consists of two layers of cells, very often contains large palosclereids which are often arranged in rows. Very large palosclereids are found in *S. bicolor* (Plate I, Fig. 2), whereas those of *S. vallicola* have the thickest walls (Plate II, Fig. 1; Plate XV, Fig. 4). The spongy parenchyma of *S. spec.*, Bang 2401, contains no sclereids at all, that of *S. vallicola* (Plate IV, Fig. 10) and *S. crassipes* rather small astrosclereids, that of *S. pachyphylla* and *S. didyma* contains astrosclereids and transitions to ophiurosclereids (Plate IV, Figs. 11–13, 15) and that of *S. bicolor* big ophiurosclereids (Plate IV, Figs. 9, 14, 22, 23). A transverse section through the leave of *S. vallicola* is given on Plate XV, Fig. 4.

The third group, which comprises the species *S. corallina*, *S. guianensis*, *S. sympetala*, two not yet described species and probably *S. peruviana*, is characterized by the presence of rhizosclereids, usually in rather larger numbers, but sometimes, e.g. in *S. sympetala*, in a small number only. In the spongy parenchyma of the species belonging to this group typical ophiurosclereids and/or librosclereids and transitions between these two types are found (Plate III, Figs. 14–28; Plate IV, Figs. 14, 18–25; Plate XV, Fig. 3).

Within the genus *Norantea* rather considerable differences in the number and shape of the sclereids are encountered. In the leaves of the species belonging to the subgenus *Sacciophyllum*, as well as those of *N. brasiliensis* and of *N. adamantium*, the sclereids are almost entirely limited to a few brachysclereids, sometimes accompanied by a few sclereids of another type in the vicinity of the midrib. This applies also to the species belonging to the subgenus *Pseudostachyum*, although the leaves of some of the species of this subgenus contain a fairly large number of palosclereids.

N. cuneifolia, *N. spiciflora* and *N. jimenensis* occupy an isolated position in this genus. The leaves of *N. cuneifolia* contain numerous palosclereids provided with rudimentary protrusions and showing therefore an approach to rhizosclereids; other kinds of sclereids are lacking. An undescribed species (Cuatrecasas 16618), probably belonging to the genus *Norantea*, resembles *N. cuneifolia* in the structure of the palosclereids, but in its spongy parenchyma large and rather irregular astrosclereidlike sclereids with a wide cell lumen are present which sometimes show an approach to idiosclereids (Plate I, Fig. 2). In *N. jimenezii* the spongy parenchyma contains rather large, irregularly shaped sclereids with disorderly and rather short protrusions and a relative thin wall (Plate I, Fig. 6). This type of sclereid is difficult to include in one of the distinguished categories. In *N. spiciflora* the palosclereids (Plate I, Fig. 7) are remarkable large, and possess a rather wide cell lumen and a thick wall; they vary strongly in size and are several times larger than the surrounding palisade cells; they show a fairly strong resemblance to the palosclereids found in *Souroubea vallicola*. The spongy parenchyma in this species contains a large number of rather densely packed idiosclereids which are oriented perpendicular to the surface (Plate I, Figs. 8, 9); they belong to a type which is well represented in the genus *Marcgravia*.

The subgenus *Marcgraviastrum* differs strongly from the other subgenera of Norantea as to the sclereids. In the leaves of all its species we find a large number of sclereids belonging to at least two types forming a pattern which lend the leaf a characteristic structure (Plate XVI). The leaves of some species, e.g. *N. brenesii*, *N. wed-*

delliana, *N. macrocarpa* and *N. costaricensis* contain rhizosclereids of type 1 as well as astrosclereids or ophiurosclereids (Plate XVI, Fig. 3), those of other species, e.g. *N. obovata*, *N. pendula*, *N. peduncularis*, *N. subsessilis* and *N. sodiroi* contain rhizosclereids of the types 1, 2 and 3, as well as librosclereids, the latter often in two tiers, immediately below the palisade layer and just above the upper epidermis (Plate XVI, Fig. 1). Sometimes, e.g. in *N. subsessilis* and in *N. sodiroi*, the leaves contain astrosclereids or ophiurosclereids and brachysclereids too (Plate XVI, Fig. 2).

The genus *Marcgravia* too contains some groups of species in which the leaves show a characteristic sclereid pattern; however they are less sharply defined than the patterns found in the other genera. The species belonging to these groups often agree in other taxonomical important characters too, but this does not apply to all of them.

Within the section *Orthothalamium* three groups may be distinguished. The first group, which comprises the species *M. angustifolia*. *M. comosa*, *M. crenata*, *M. macrophylla*, *M. magnibracteata*, *M. mexicana*, and *M. spec.*, Skutch 3762 is characterised by the presence of numerous regularly spread or sometimes scattered idiosclereids which are usually elongated and not at all or only slightly ramified, provided with a rather narrow cell lumen and a thick wall and which are oriented perpendicular to the surface of the leaf (Plate XIV, Figs. 1,2).

In the second group which is formed by *M. brownei*, *M. myriostigma*, *M. goudotiana*, *M. schippii* and *M. spec.*, Cuatrecasas 16890 the leaves contain a large number of osteosclereids which are separated from each other by small intervals and which connect the lower epidermis with the upper one as pillars (Plate XIV, Fig. 5).

The third group, which is less uniform than the two other ones, consists of the species *M. flagellaris*, *M. leticiana*, *M. rectiflora*, *M. trinitensis*, *M. spec.*, Aristeguieta 4460, *M. spec.*, Cowan 38207 and *M. spec.* Mexia 7109. Here we usually find a large number of irregularly branched sclereids which form a dense network. *M. rectiflora*, which in other respects agrees well with the species of this group, is provided with sclereids which show a much less differentiated form (Plate IX, Figs. 4, 5); their projections are shorter than those of the sclereids of the other species of the group with the result that these sclereids are quite free from each other; they form, therefore, a pattern which shows a stronger resemblance to that found in the first group. In *M. trinitatis* the sclereids are provided with long branches and projections spreading in all directions; there is a slight indication that part of them are oriented more or less perpendicular to the surface of the leaf, whereas another part runs more or less parallel to the latter (Plate IX, Figs. 6, 7; Plate XI, Fig. 9). In the other species this difference in orientation is more pronounced; the sclereids which are oriented parallel to the surface run mainly in the longitudinal direction of the leaf. The sclereids in these species are all very irregular in form, and remind us of rhizosclereids, ophiurosclereids and librosclereids (Plates X, XI). Together they form a dense tangle in which the individual cells are hardly recognizable (Plate XIV, Figs. 3, 4).

In most of the species belonging to the section *Plagiothalamium* the leaves chiefly contain idiosclereids which although differing in form, size and number, do not form such marked patterns as are found in the section *Orthothalamium*. *M. coriacea* and its allies as e.g. *M. romaimana* and *M. williamsii*, nevertheless form a distinct group. Their sclereids are large, irregularly shaped idiosclereids, provided with a wide cell lumen and many rather long projections (Plate VII, Figs. 9, 13-15). The distances by which they are separated from each other are small, and occasionally, e.g. in *M. coriacea* and in *M. williamsii*, they are arranged more or less in two tiers (Plate XV, Fig. 2). The sclereids of *M. spec.*, Cuatrecasas and Killip 39100, seem to be somewhat longer (Plate VII, Fig. 15), and those of *M. roraimana* are, as a rule, somewhat smaller, provided with lesser and shorter projections and with a narrower cell lumen than the preceeding species.

Among the remaining species of the section *Plagiothalamium* a number have but few or hardly any sclereids in their leaves; those present look more or less like brachysclereids or transitions from the latter to astrosclereids or idiosclereids, and are found near the midrib; if their number is somewhat larger, they may be spread throughout the leaf, and in this case they belong to the category of the idiosclereids (some of the latter are shown in Plate VII, Figs. 5, 6, 10, 11, 12 and 16). To this group of species, which however is not yet thoroughly studied, belong among others the species *M. parviflora*, *M. gracilis*, *M. purpurea*, *M. pedunculosa*, *M. weberbaueri* and *M. eichleriana*. The sclereid pattern of these group remind us, if sclereids are present, of that found in the first group of the section *Orthothalamium*. In a number of species, e.g. *M. evenia*, *M. domingensis*, *M. sintenisii* and *M. lineolata*, the sclereids are somewhat more robust (Plate VII, Figs. 17, 18, and 19), more numerous and therefore nearer to each other. *M. spec.*, Fanshawe and Maguire 23467, differs from the other species by the presence of a pecular type of brachysclereid which is provided with a thin wall and a large cell lumen (Plate VII, Fig. 7); they are rather numerous and regularly distributed in the leaf. Similar sclereids are met with in *M. soropaniana*, but here they are found only in the vicinity of the midrib and here in a small number only. *M. gentlei* has rather characteristic astrosclereids in its leaves; they show a wide cell lumen (Plate VII, Fig. 8); and *M. waferi* differs from the other species in its astrosclereid-like sclereids which, especially in the vicinity of the midrib, are provided with long projections.

COMPARISON OF THE FOLIAR SCLEREIDS OF THE MARCGRAVIACEAE WITH THOSE FOUND IN SOME OTHER FAMILIES

As already mentioned foliar sclereids are found in a great number of families. In few families however they are such an important feature as in the *Marcgraviaceae*, this is e.g. the case in the *Theaceae* (WIJNAENDTS FRANCKEN, 1890; PEKELHARING, 1908; CAVARA, 1897;

BEAUVISAGE, 1920; FOSTER, 1944; RAO, 1952; BARUA and WIGHT, 1959; BARUA and DUTTA, 1960; KENG, 1962), the *Proteaceae* (JÖNSSON, 1880; WIJNAENDTS FRANCKEN, 1890; TSCHIRCH, 1881; RAO, 1950b); the Oleaceae (TSCHIRCH, 1881, 1885; KRISHNASWAMY 1942; RAO, 1947, 1948, 1949, 1950a, 1957b; RAO and KULKARNY, 1952; ARZEE, 1953a, b) and the genera *Mouriria* and *Memecylon* of the Melastomataceae (VAN TIEGHEM, 1891; FOSTER, 1946, 1947; SUBRAHMANYAN and RAO, 1949; RAO, 1950b, 1951c, 1957a; MORLEY, 1953; RAO and DAKSHNI, 1963), although in none of these families do they show such a variation in form and pattern as they do in the *Marcgraviaceae*.

Brachysclereids or stone cells are widely distributed and so well known that it is not necessary to give examples.

Astrosclereids are well known too, typical astrosclereids are e.g. those found in the *Nymphaeaceae* (MALAVIYA, 1962).

Ophiurosclereids which show a strong resemblance to those of the *Marcgraviaceae* are found in the leaves of the Proteacea *Isopogon petrophiloides* R. Br. (JÖNSSON, 1880; SOLEREDER, 1899, fig. 173B; ENGLER, 1894, fig. 89C).

Long straight librosclereids as occur in the leaves and the cortex of the shoots of many species of the *Marcgraviaceae* are rare in other families. They are known from the cortex and the leaves of *Pelliciera rhizophorae* Tr. et Pl. (SOLEREDER, 1899; BEAUVISAGE, 1920) and from *Araceae*, especially *Monsteroideae* (VAN TIEGHEM, 1866; RICHTER, 1899; BLOCH, 1947; NICOLSON, 1960). Long filiform sclereids are e.g. known from species of *Mouriria* (FOSTER, 1946, figs. 22–30, 39) and *Memecylon* (RAO, 1951c, 1957a), from *Olea europaea* L. (TSCHIRCH, 1881; ARZEE, 1953a), from species of *Linociera* (RAO, 1957b) and from some *Annonaceae* (RAO and WEE, 1966), but these sclereids are bent and twisted irregularly and usually they run in a criss-cross manner through the leaf. Some authors (e.g. KAUSMANN, 1963) regard this type of sclereids as fibers.

Sclereids which show much resemblance to the idiosclereids found in *Norantea spiciflora* and many species of *Marcgravia* are known from the leaves of a great number of species belonging to different families. These sclereids are often indicated as astrosclereids and sometimes as polymorphic sclereids. This type of sclereid is common in the *Theaceae*; they are found e.g. in various species of the genera *Ternstroemia* (BEAUVISAGE, 1920, figs. 11 and 12) and *Camellia* (TSCHIRCH, 1889, fig. 348; BARUA and WIGHT, 1959, figs. 9 and 10; BARUA and DUTTA, 1960). Other species from which idiosclereid-like sclereids are known are e.g. the Rhizophoracea *Rhizophora conjugata* L. (SOLEREDER, 1899, fig. 74A; METCALF and CHALK, 1950, fig. 133A), the Capparidacea *Niehbuhria apetala* Dunn (RAO and KELKAR, 1951, figs. 1–14), the Proteacea *Leucospermum hypophyllum* R. Br. (RAO, 1950b, fig. 2), the Oleaceae *Linociera macrophylla* Wall and *L. intermedia* Wight (RAO, 1950a, figs. 1–20).

Osteosclereids extending in the leaf from the lower epidermis to the upper one are found in several families where they show a rather great diversity in form and structure. In the leaves of some species e.g. in the genus *Camellia*, osteosclereids are found together with idiosclereids, whereby the only difference between these types is that the latter do not reach the epidermis (TSCHIRCH, 1889, fig. 348). Species from which foliar osteosclereids are described are e.g. the Theaceae *Camellia thea* Link. (TSCHIRCH, 1889, fig. 348), *C. irrawadiensis* Barue (BARUA and WIGHT, 1959, figs. 1–8, fig. 11), *Gordonia lasianthus* L. (BEAUVISAGE, 1920, fig. 54), *Lacanthea pubescens* L'Hér. (BEAUVISAGE, 1920, fig. 52), and *Schima noronhae* Reinw. (BEAUVISAGE, 1920, fig. 46), the Cornacea *Nyssa caroliniana* Poir. (SOLEREDER, 1899, fig. 99A; METCALF and CHALK, 1950, fig. 174A), the Capparidacea *Capparis odoratissima* Jacq. (SOLEREDER, 1899, fig. 18B; METCALF and CHALK, 1950, fig. 24B), the Oleacea *Olea dioica* Roxb. (KRISHNASWAMY, 1942, figs. 1 and 2; RAO, 1951a, fig. 4; RAO and KULKARNY, 1952, figs. 12, 13 and 17), the Proteacea *Hakea suaveolens* R. Br. (TSCHIRCH, 1881, fig. 23) the Annonacea *Popowia pisocarpa* (Bl.) Endl. and the Melastomataceae *Mouriria cauliflora* DC., *M. pusa* Gardn. and *M. huberi* Gogn. (FOSTER, 1946, figs. 35, 36 and 37; FOSTER, 1947) and *Memecylon scutellatum* (Lour) Naud. and *M. cuneatum* Thw. (RAO, 1957a, figs. 34 and 35). In particular the sclereids found in the leaves of the three species of *Mouriria* mentioned above and in *Schima noronhae* remind us strongly of those found in *Marcgravia brownei* and its allies (Plate XII). In *Olea dioica* the osteosclereids branch at both ends with long projections running under the epidermis.

Palosclereids and rhizosclereids of the kind found in the genera *Ruyschia*, *Souroubea* and *Norantea* are probably rare in other families. Typical palosclereids are found in the leaves of the Oleacea *Nyctanthes arbor-tristis* L. (RAO, 1947, fig. 1; RAO, 1951a, fig. 2). Palosclereids showing a strong resemblance to those figured on Plate I, Fig. 2 are known from the Theacea *Freziera undulata* Sw. (SOLEREDER, 1899, fig. 29B; METCALF and CHALK, 1950, fig. 44B). Palosclereids somewhat extending into the spongy region are described from the leaves of the Ebenacea *Diospyros discolor* Willd. (RAO, 1951b) which sclereids however are developed from initials situated in the spongy region of the leaves. More or less true rhizosclereids, i.e. sclereids of the palisade layer with rootlike projections extending into the spongy parenchyma are met with in the leaves of the Theaceae *Adinandra jackiana* Korth. and *A. dumosa* Jacq. (BEAUVISAGE, 1920, Figs. 21 and 23) and *Cleyera grandiflora* Hook. f. et Thoms. (SOLEREDER, 1899, figs. 29C and D; METCALF and CHALK, 1950, figs. 44C and D).

A remarkable type of 'T' shaped sclereids is described from the leaves of *Olea europaea* L. (ARZEE, 1953a). They have a basal part with the size of a palisade cell in the palisade layer, no projections into the spongy region but two very long projections running underneath the epidermis (ARZEE, 1953a, figs. 4–6 and 8H).

Not only the sclereids but also the sclereid patterns found in many species of *Marcgravia* find a counterpart in those found in species of other families. Several *Theaceae* have a foliar sclereid pattern similar to that found in one or more species of *Marcgravia*. The intricate network of filiform sclereids observed in the leaves of e.g.

Mouriria anomala Pulle and its allies (Foster, 1946, plate VII-IX) and *Olea europaea* L. (Tschirch, 1881, fig. 22; 1885, fig. 31; Arzee, 1953a, figs. 1 and 2) show a superficial resemblance to the patterns of tangled sclereids as are found in *Marcgravia flagellaris* and related species where, however, the sclereids show a greater diversity in form.

The sections through the leaves of *Schima noronhae* Reinw., *Mouriria pusa* Gardn. and *Memecylon scutellatum* (Lour) Naud. and *M. cuneatum* Thw. (Rao, 1957a, figs. 34 and 35) respectively figured by Beauvisage (1920, fig. 46) and Foster (1946, fig. 16), show a striking resemblance in sclereid pattern to *Marcgravia brownei* (Plate XIV, Fig. 5).

The sclereid patterns composed of different types of sclereids as are found in the genera *Ruyschia*, *Souroubea* and *Norantea* subgenus *Marcgraviastrum*, however form a feature confined to the leaves of these *Marcgraviaceae*.

The systematic value of sclereids

Opinions about the systematic value of sclereids found in the literature are rather contradictory and in most cases guardedly formulated. Solereder (1899) and Van Tieghem (1891) adjudged the sclereids to be of value at the specific level. Bailey and Nast (1944) in their study on the *Winteraceae*, point to the instability and variability of internal characters of the leaf and the consequential danger in using them for taxonomic purposes. Morley (1953) made an extensive study of the systematic anatomy of the genus *Mouriria*. He concluded that the great variety of form in the genus and the relative consistency of form within the species make sclereid morphology a very valuable diagnostic character. The more distinct types will sometimes indicate the section and even the species of a specimen. However, owing to the occurrence of like forms in different sections and the tendency of the majority of the species in a section to have much the same sclereid morphology, this character, like most others, cannot be relied upon alone, but must be used in conjunction with one or more other characters. Rao (1957), who contributed very much to our knowledge of foliar sclereids, in his study on *Memecylon* states that though a cautious use of this character is needed, the sclereids should form a part of any thorough taxonomic analysis. Keng (1962) in his study on the anatomy of the *Theaceae* stated that in general the presence or absence and the shape and the size of foliar sclereids seem to be rather constant characters. Species of the same genus, with few exceptions, have essentially similar patterns of sclereids and this similarity is also found among many species of different but related genera. Barua and Dutta (1960) found that three varieties of *Camellia sinensis* are characterised by the form and the number of the foliar sclereids. In these taxa the form of the sclereids appeared to be a useful taxonomic character which appeared to be correlated with the presence or absence of taxonomically important chemical substances. In Camellia the sclereids seem to be a valuable taxonomic character at the specific as well as at the infra-specific level. Nicolson (1960) on the contrary found that in the *Monsteroideae* the distribution and frequency of trichosclereids in various organs of a given species may not be constant and that presence or absence of trichosclereids should not be used alone as a diagnostic or key character at any classification level in *Araceae*.

The results of my study of the foliar sclereids of the *Marcgraviaceae* lead to conclusions which in general agree with those of most of the above mentioned authors. In the *Marcgraviaceae* the difference in form and pattern of the sclereids among different specimens of the same species is probably only slight in most species but in some species it may be rather considerable. In only few species, however, could this variation be studied more or less satisfactorily. In *Souroubea guianensis*, a wide spread species, there exists a rather great variation in form and number of the sclereids and especially in the ratio of the different types. The sclereid pattern in this species consists of rhizosclereids combined with ophiurosclereids, librosclereids and transitional forms between the last two categories. There exists a variation in the form and the density of the rhizosclereids and in the ratio between ophiurosclereids and librosclereids which varies from nearly 100% librosclereids to nearly 100% ophiurosclereids. This difference in sclereid pattern is correlated with differences in other characters and therefore can serve as a basis for the subdivision of the species. In some species of the *Marcgraviaceae* the form or structure of the sclereids or the sclereid pattern is so characteristic that the species is easily recognisable by it, but often related species show less difference in form or pattern of the sclereids. The complete variation in form and pattern of sclereids in the species of the *Marcgraviaceae* needs further investigation. A number of groups of species appear to have a similar sclereid pattern which is correlated with other characters. As already mentioned there exist great differences in sclereid forms and patterns between *Marcgravia* and the other genera. In the *Marcgraviaceae* the sclereid pattern forms, in general, a good character in defining species, sections and even genera. However, as it happens in nearly every taxonomic unit, like a section or a genus, that one or more species deviate in this character from the general trend – a phenomenon which may present itself also in other characters – it is advisable to use this character only in combination with others. Taxonomy can never be based on a single character but only on the totality of the characters, an opinion generally accepted but often forgotten in practice. The overestimation of a character, as is done by Richter (1920) with regard to the sclereids of the *Marcgraviaceae*, may lead to a highly unnatural classification as is found e.g. in his subdivision of the genus *Norantea*.

Our conclusion must be that it is difficult to ascertain the real value of foliar sclereids as a taxonomic character, especially the value which can be attached to quantitative differences. It is absolutely necessary to have sufficient data about the possible variation of form, frequency and distribution of the sclereids in the leaves of the individual plant as well as in the species before conclusions can be made. It is still questionable whether and to what extent form, frequency and distribution of sclereids are influenced by environmental factors. To gain a better view and a more funded opinion on this problem it is necessary to know what internal or external factors might play a role, either directly or indirectly, in the initiation and ontogeny of sclereids. It is therefore that experiments as those of FOARD (1958, 1959) and of AL-TALIB and TORREY (1961) are of great interest for the taxonomist too, though they are only the first step towards the solution of the problems.

THE FUNCTION OF FOLIAR SCLEREIDS

A discussion of the problem of the possible functions of foliar sclereids is given by RAO (1957b), to which we also referred for a review of the literature. An excellent treatment of the mechanical functions of sclereids is given by WIJNAENDTS FRANCKEN (1890). In many cases the mechanical function of the sclereids is evident, with regard to the *Marcgraviaceae*, this has already been observed by RICHTER (1920). Sclereid patterns, particularly as figured on the Plates XIV, Figs. 3, 4; XV, Fig. 3 and XVI, Fig. 1–3, give these leaves great strength.

TSCHIRCH (1881) was of the opinion that the presence of foliar sclereids in many species is an adaption of the plants to a dry environment because they help to prevent the deformation of the leaf and especially of the photosynthetic tissue by a temporary desiccation. Examples to illustrate this are found in many *Oleaceae* and *Proteaceae*.

Although the *Marcgraviaceae* are all inhabitants of regions with a wet climate it is not impossible that the above mentioned opinion of Tschirch applies to at least a part of the *Marcgraviaceae* provided with foliar sclereids too. This may be the case in the species which by their epiphytic habitat are exposed to short periods of drought and in the species from e.g. montane rain forests where owing to the low temperature and often strong winds one might speak of a physiological drought. The question of the function of foliar sclereids, however, needs further investigation, both as to the suggested mechanical function and as to possible other functions e.g. that of water storage cells.

EXPLANATION OF PLATES

PLATE I

Sclereids of *Norantea* species. Palosclereids from the palisade parenchyma are figured as they appear to us seen through the epidermis of the cleared leaf and in transverse sections. Fig. 1 — *N. cuneifolia* Delp., Gardner 333, palosclereids.Figs. 2, 5 — *N. spec.*, Cuatrecasas 16618; Fig. 2: palosclereids; Fig. 5: sclereids from the spongy mesophyll. Figs. 3, 4 — *N. spec.*, Phelps & Hitchcock 422; Fig. 3: palosclereids; Fig. 4: sclerified cells from the spongy parenchyma. Fig. 6 — *N. jimenezii* (Standley) de Roon, Standley & Valerio 49160, sclereids from the spongy mesophyll. Figs. 7, 8 — *N. spiciflora* (Juss.) Kr. et Urb., Stehlé 328; Fig. 7: palosclereids; Fig. 8: idiosclereids.

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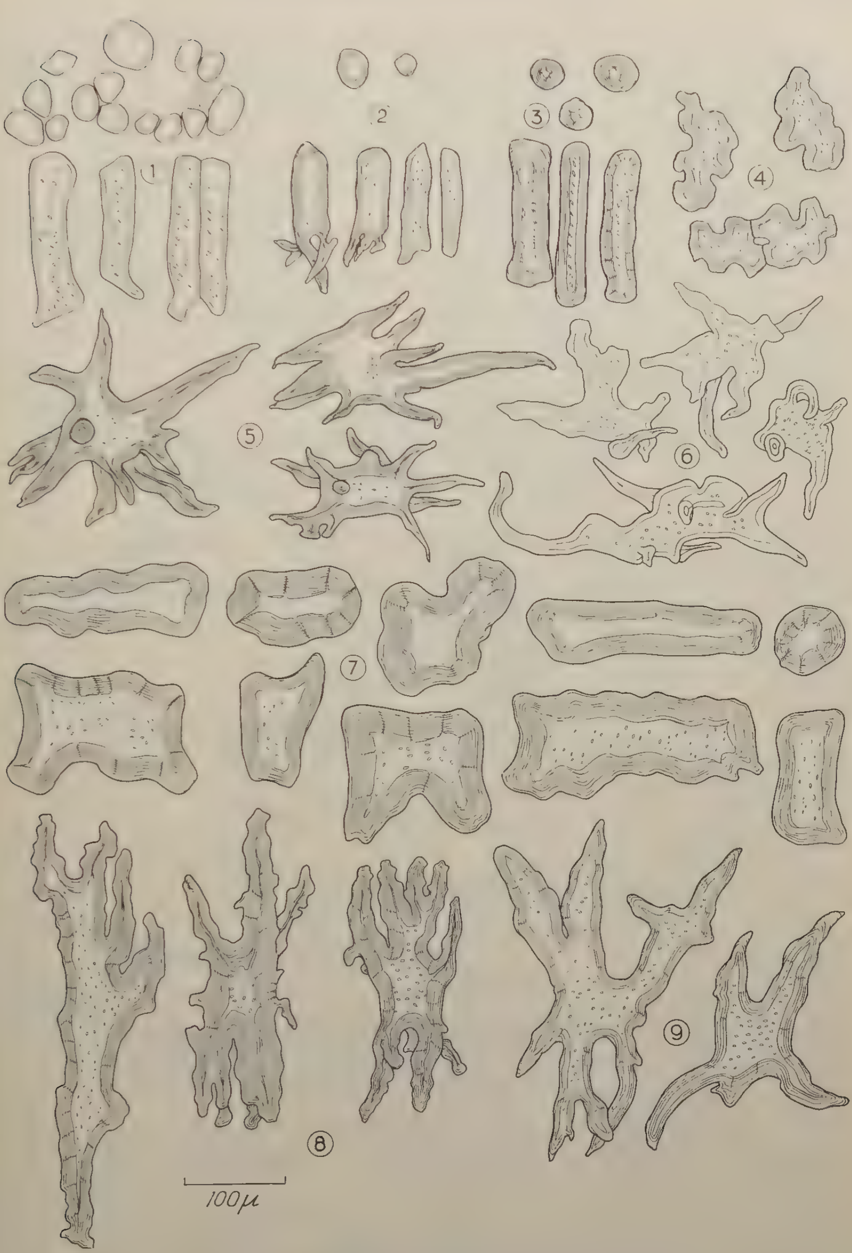


PLATE I Foliar sclereids of Norantea species

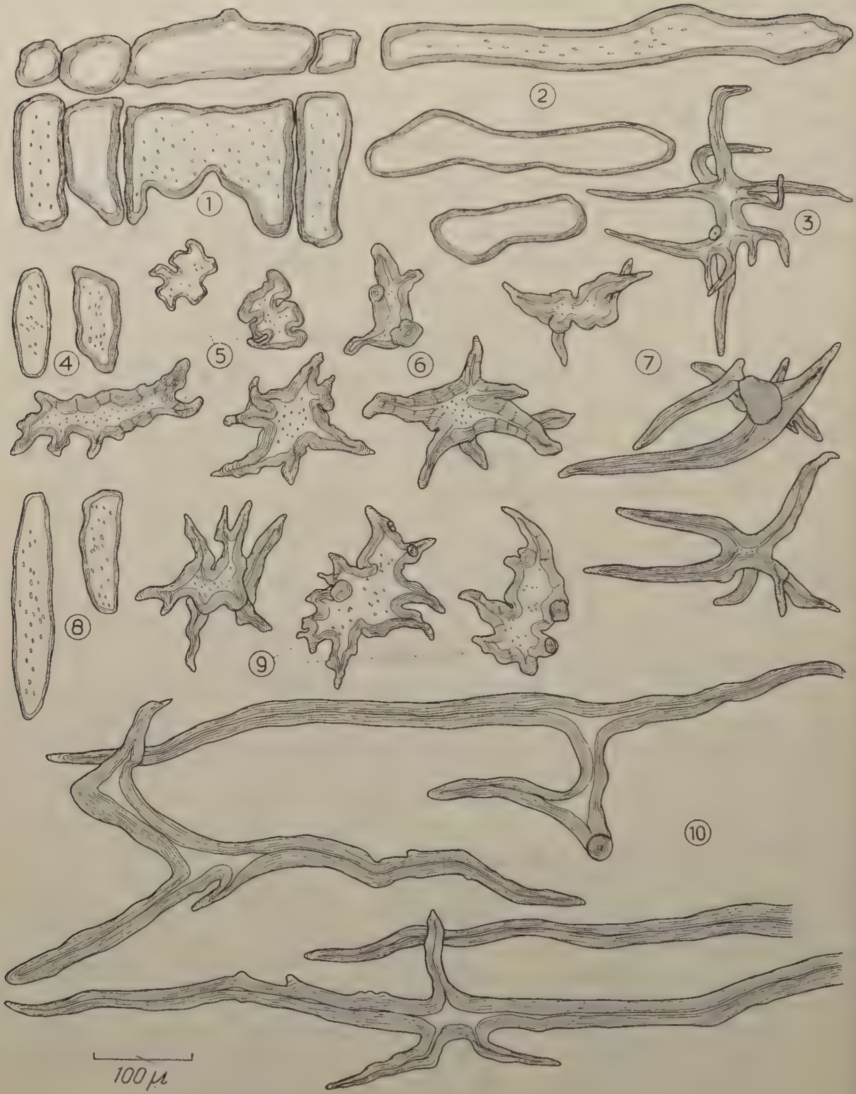


PLATE II Foliar sclereids of Souroubea species

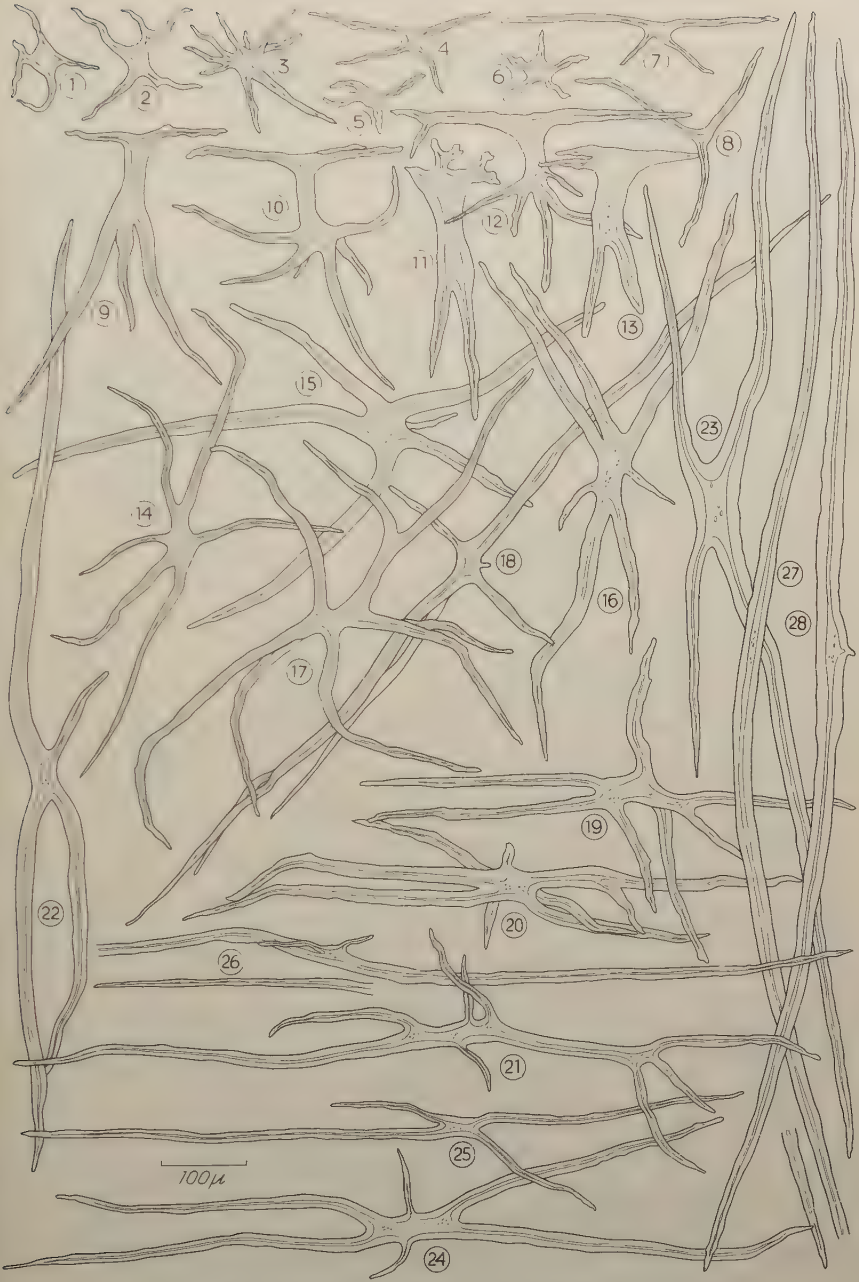


PLATE III Foliar sclereids of Souroubea guianensis

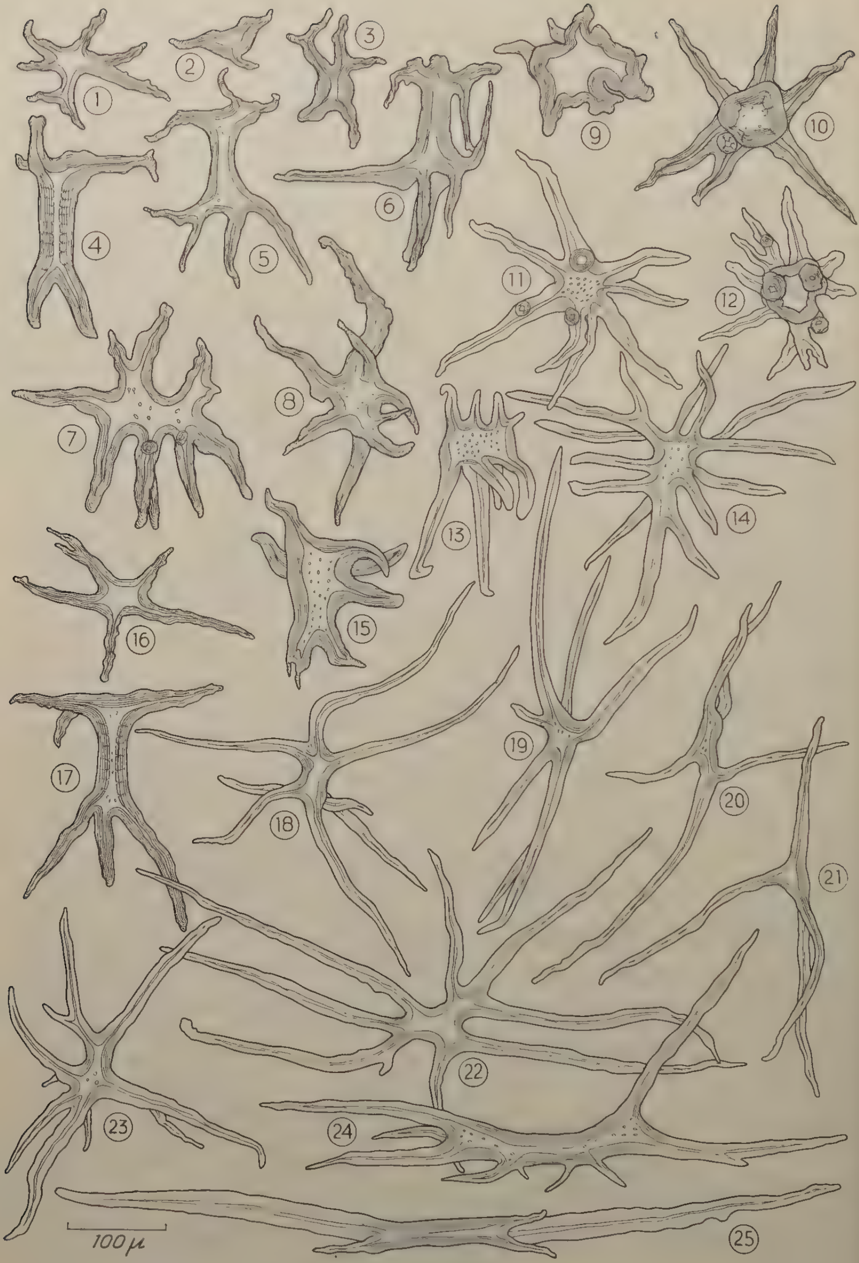


PLATE IV Foliar sclereids of Ruyschia and Souroubea species

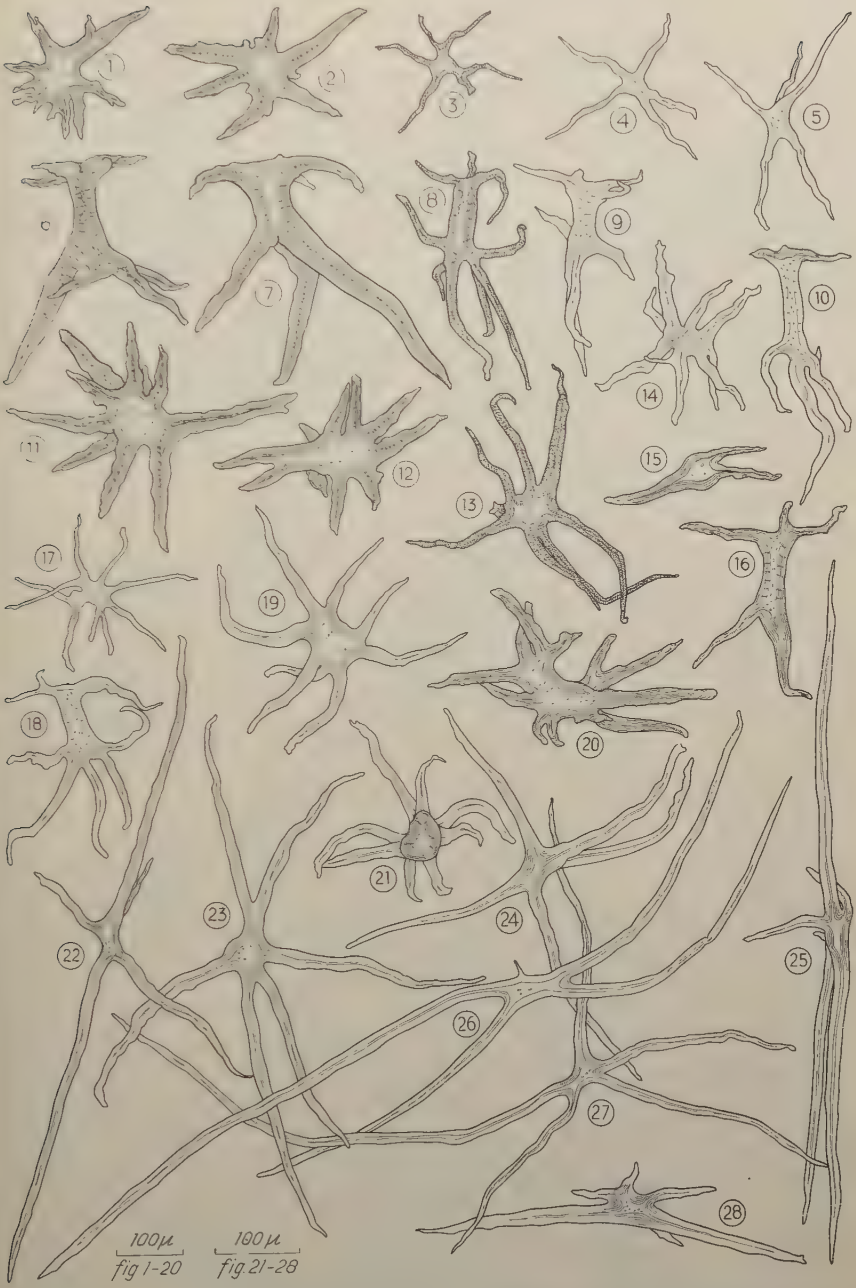


PLATE V Foliar sclereids of species of Norantea subg. Marcgraviastrum

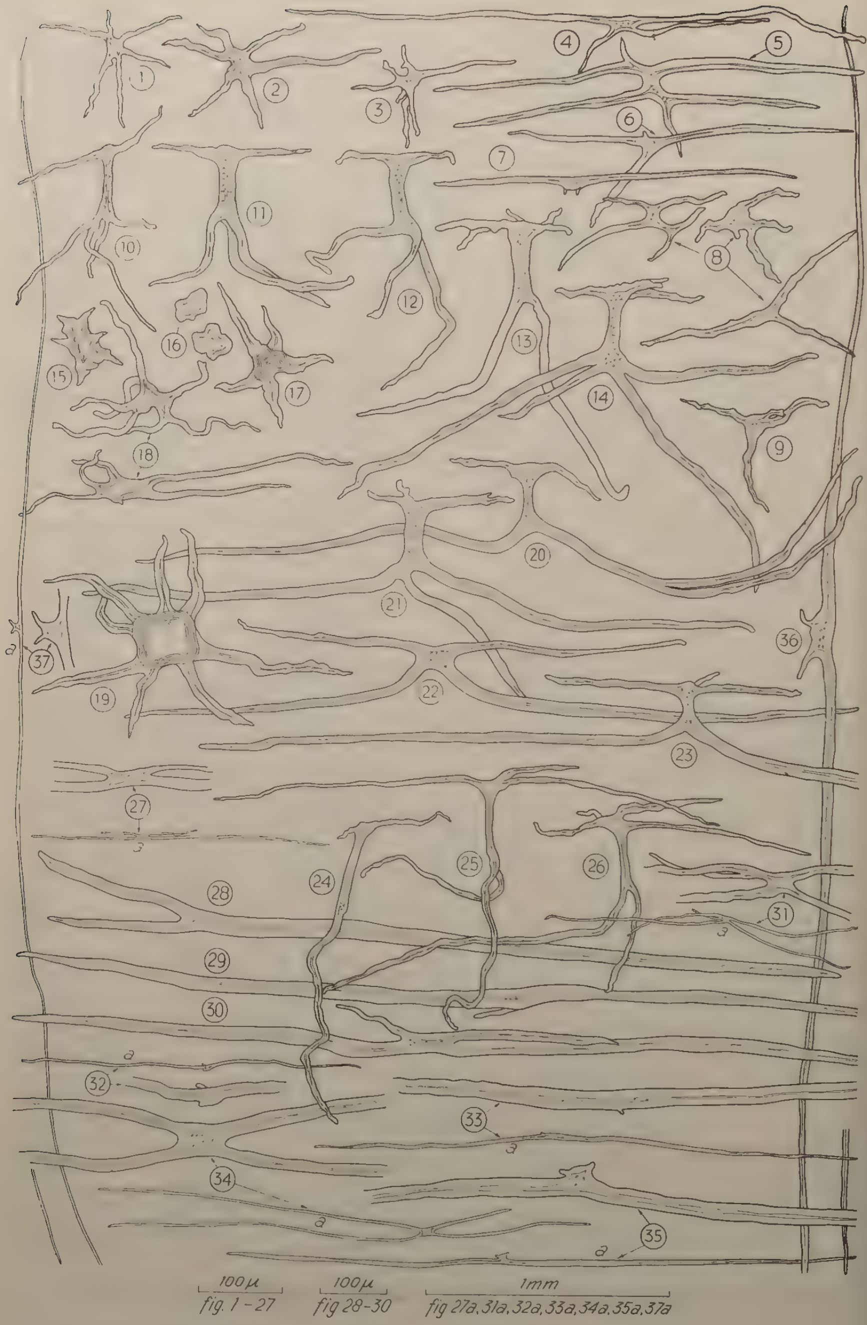


PLATE VI Foliar sclereids of species of Norantea subg. Marcgraviastrum

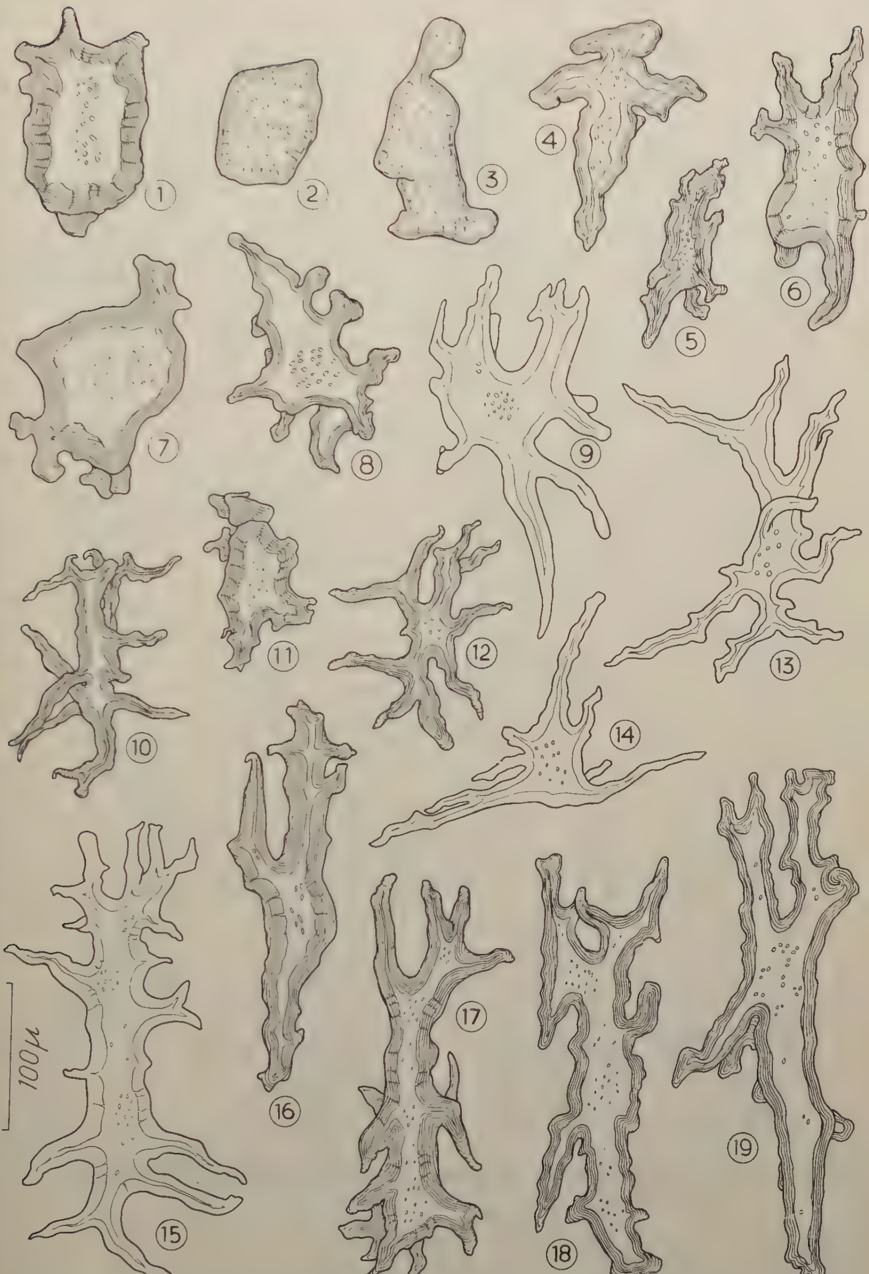


PLATE VII Foliar sclereids of species of Marcgravia sect. Plagiothalamium

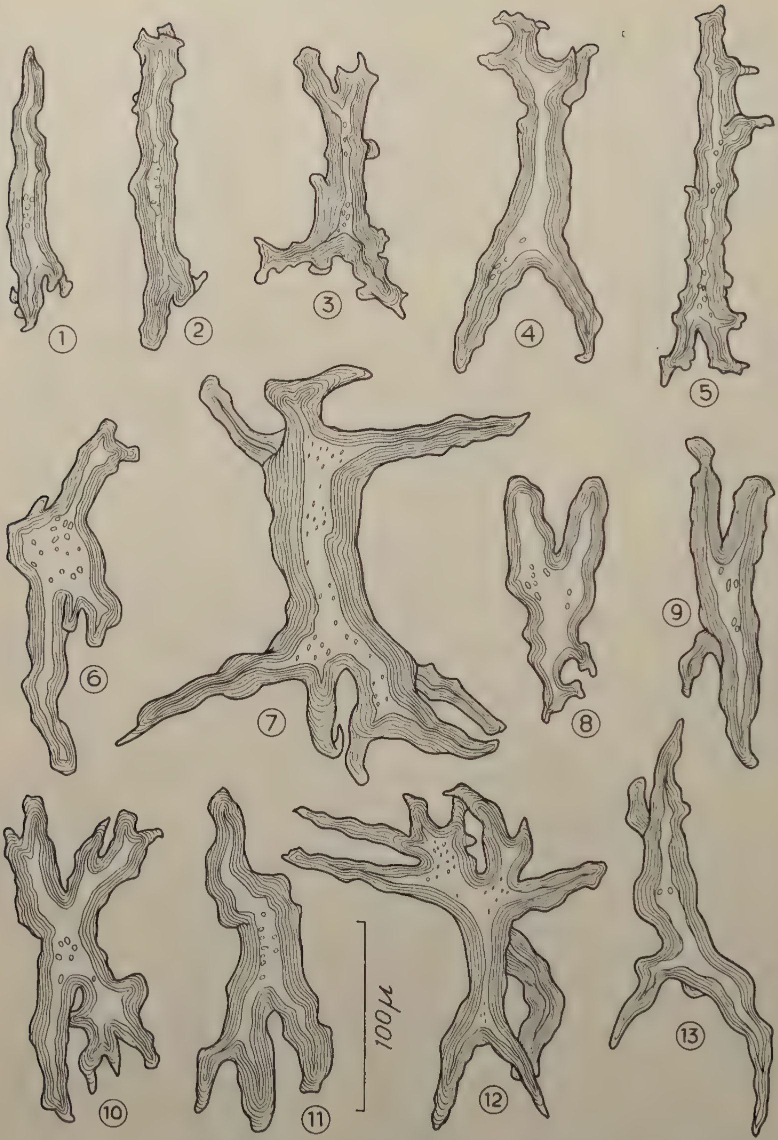


PLATE VIII Foliar sclereids of species of Marcgravia sect. Orthothalamium

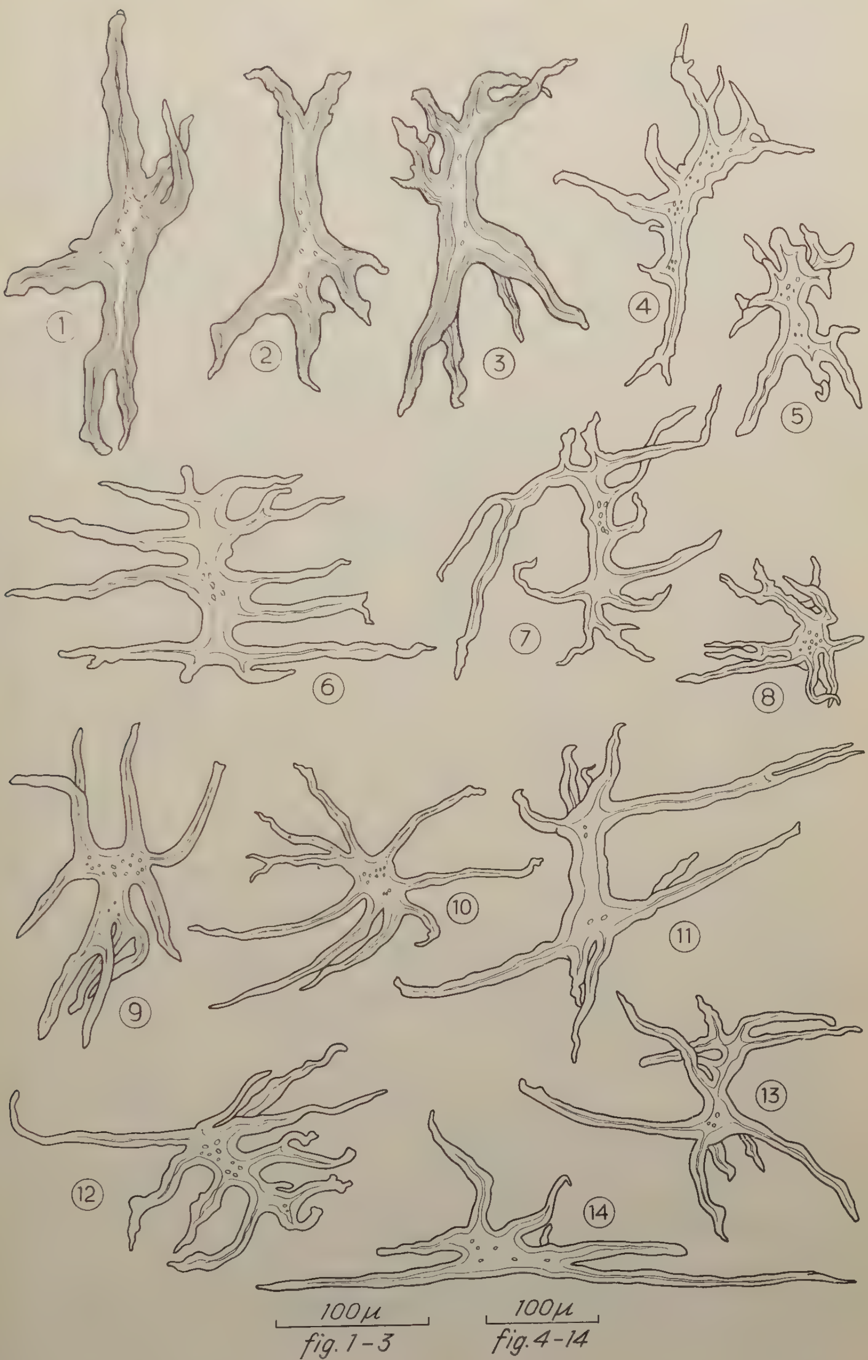


PLATE IX Foliar sclereids of species of Marcgravia sect. Orthothalamium

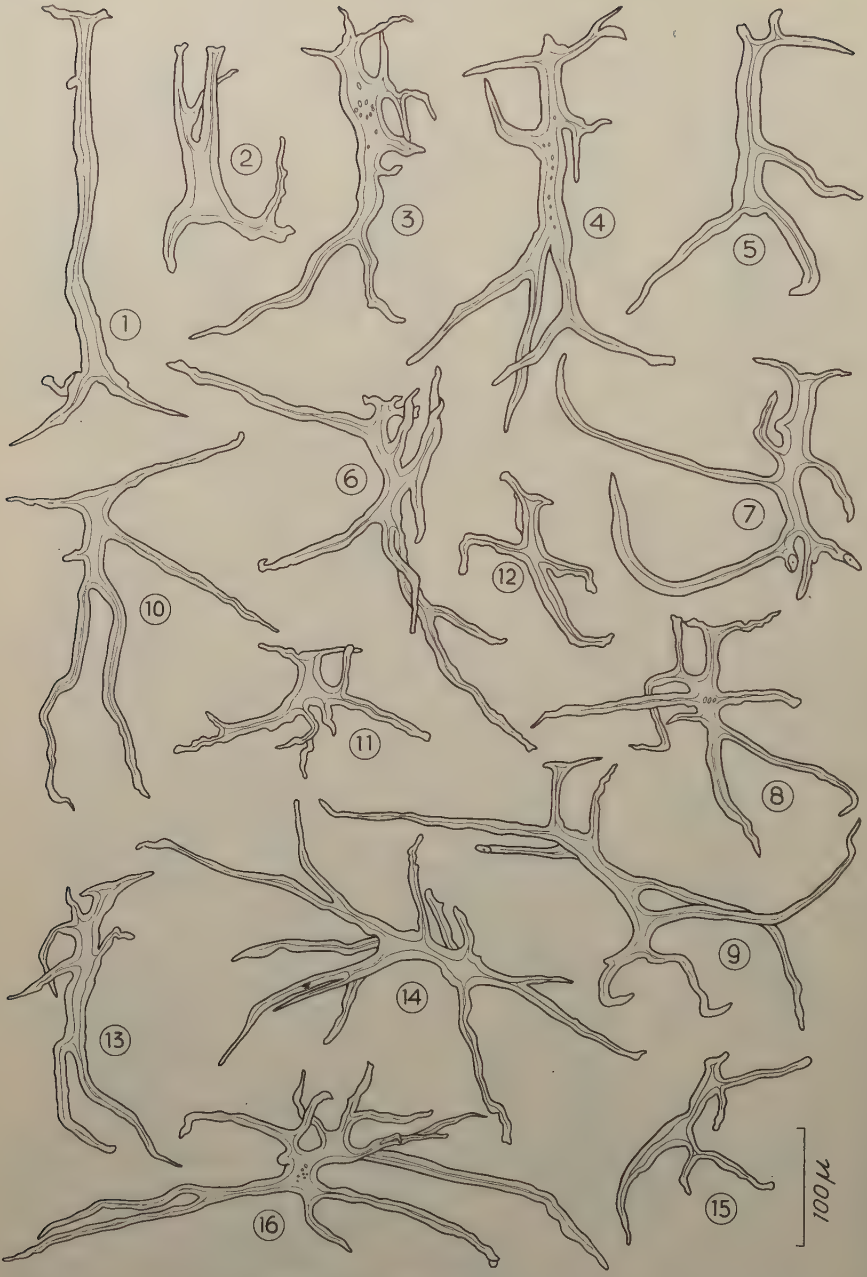


PLATE X Foliar sclereids of species of Marcgravia sect. Orthothalamium

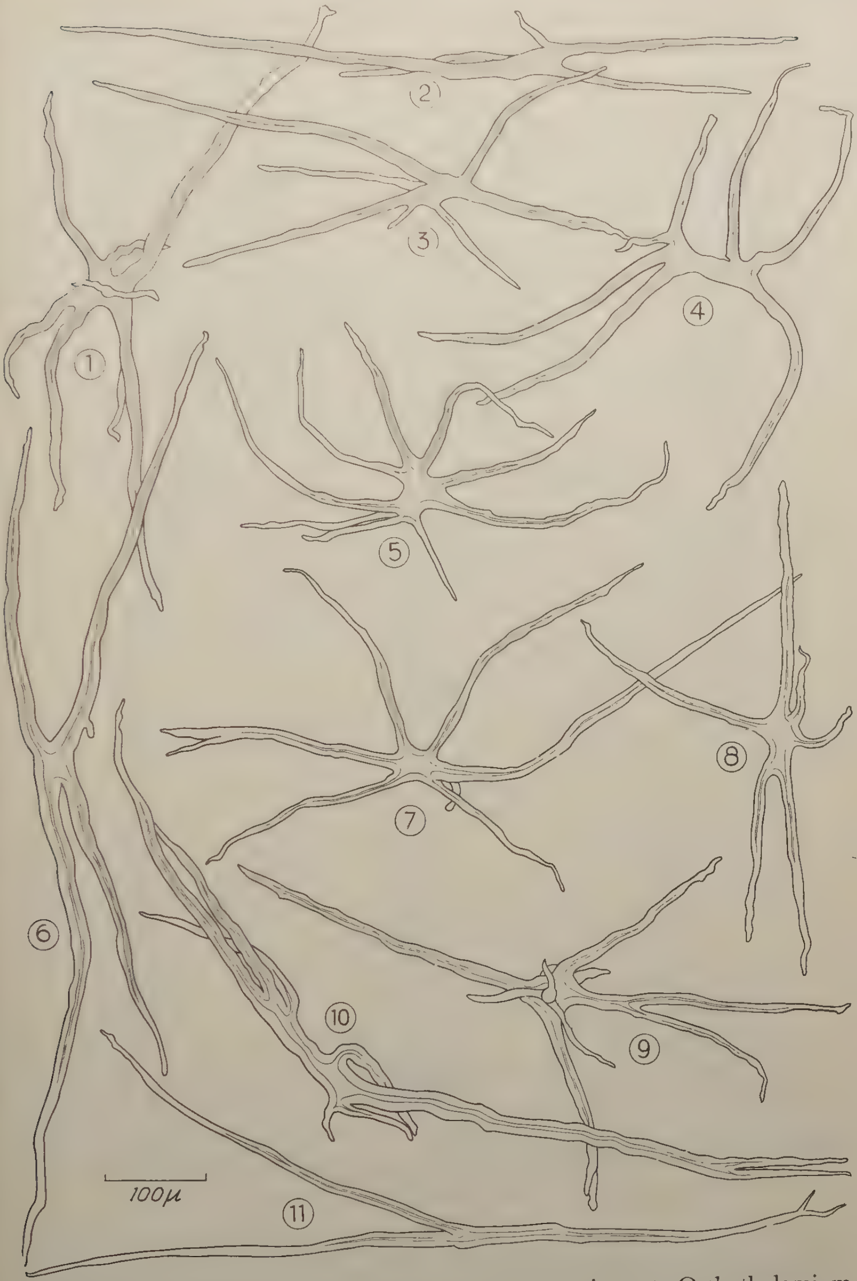


PLATE XI Foliar sclereids of species of Marcgravia sect. Orthothalamium

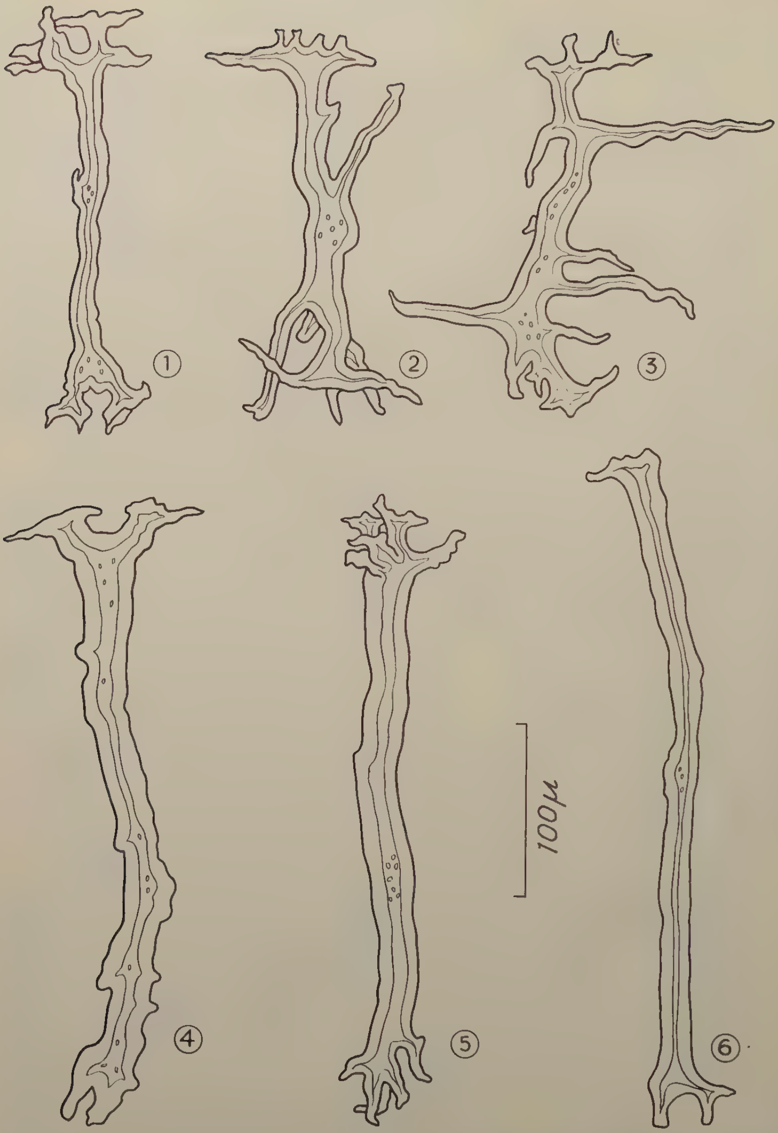


PLATE XII Foliar sclereids of species of Marcgravia sect. Orthothalamium

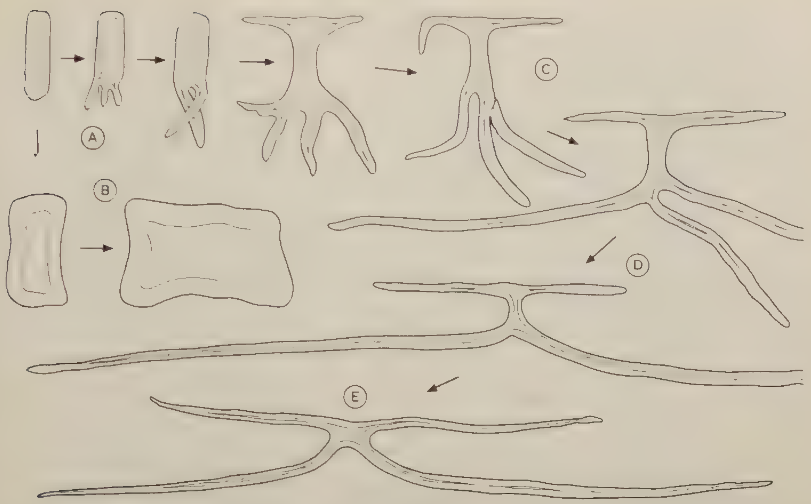


Fig. 1

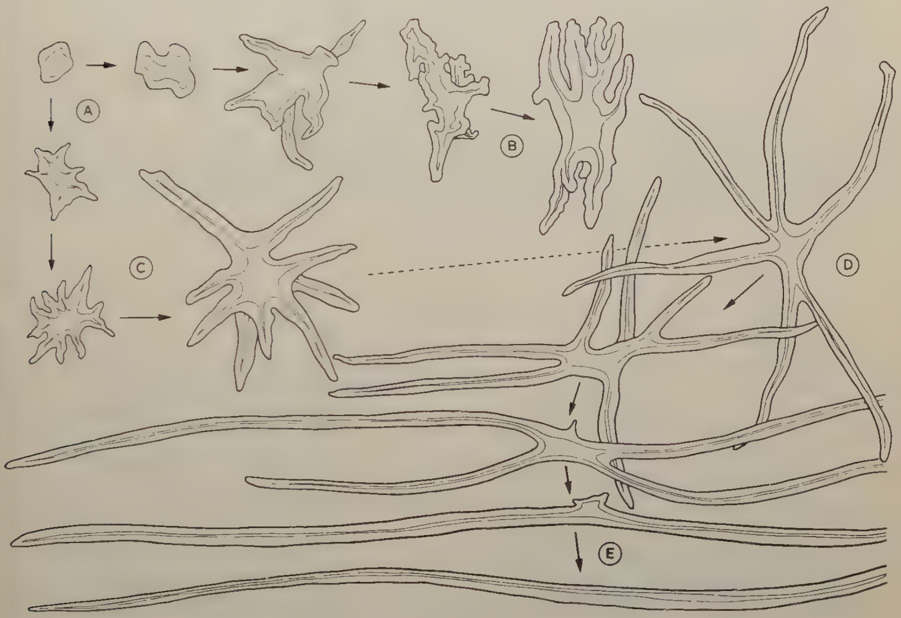
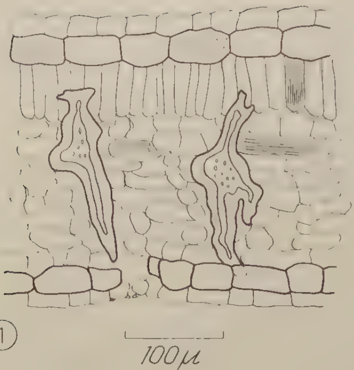


Fig. 2

PLATE XIII Fig. 1. Morphological series showing the derivation of the types of sclereids from the palisade parenchyma in the genera Ruyschia, Souroubea and Norantea. Fig. 2. Morphological series showing the derivation of the types of sclereids from the spongy parenchyma in the genera Ruyschia, Souroubea and Norantea.



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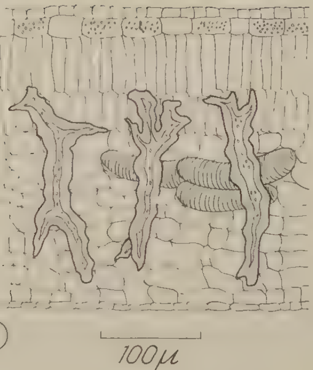

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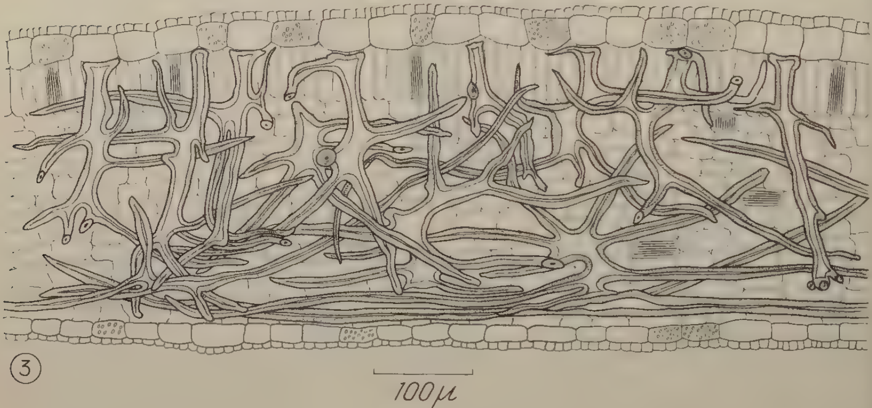

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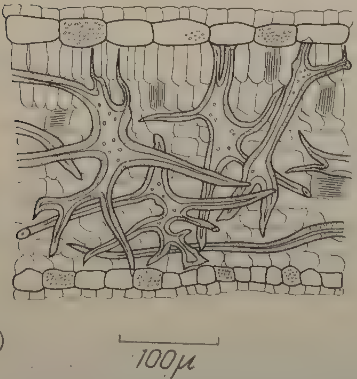

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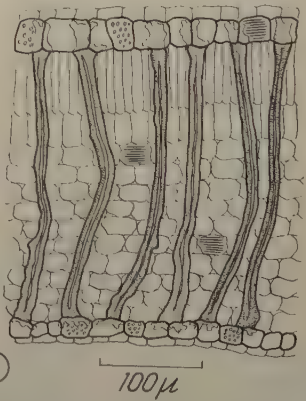

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PLATE XIV Transverse sections through the leaves of Marcgravia mexicana (Fig. 1), M. magnibracteata (Fig. 2), M. leticiana (Fig. 3), M. spec. (Fig. 4) and M. brownei (Fig. 5) showing the sclereid pattern. Semidiagrammatic.

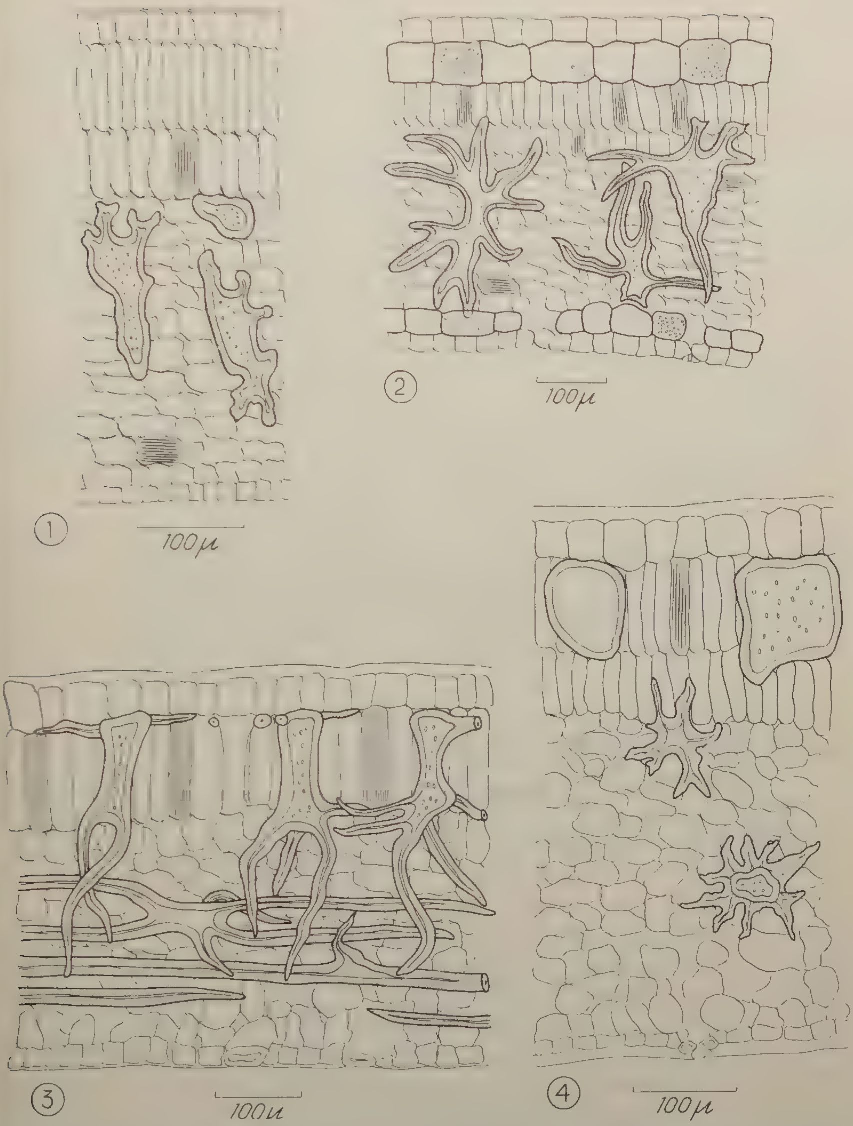

PLATE XV Transverse sections through the leaves of Marcgravia gentlei (Fig. 1,) M. coriacea (Fig. 2), Souroubea guianensis (Fig. 3) and S. vallicola (Fig. 4) showing the sclereid pattern. Semidiagrammatic.

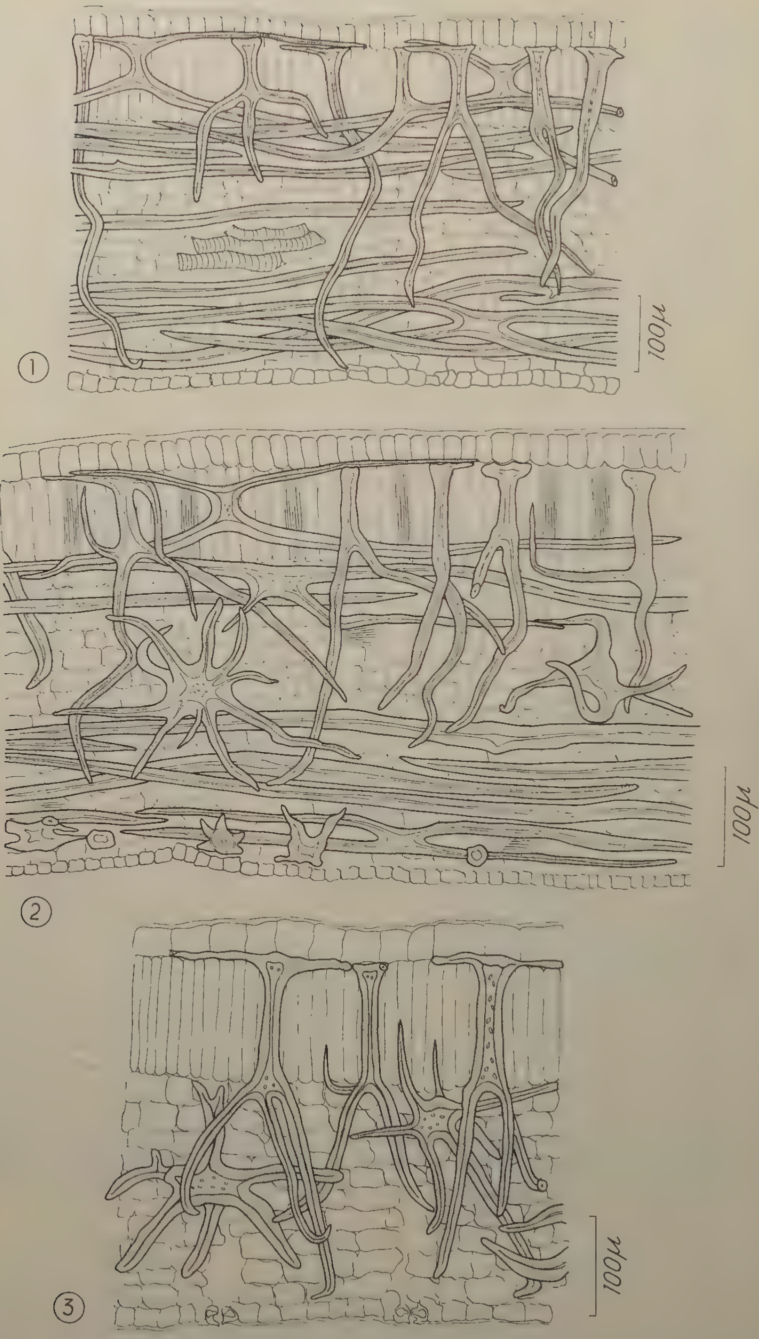

PLATE XVI Transverse sections through the leaves of Norantea peduncularis (Fig. 1), N. sodiroi (Fig. 2) and N. weddelliana (Fig. 3) showing the sclereid pattern. Semidiagrammatic.

EXPLANATION OF PLATES (continued)

PLATE II

Sclereids of *Souroubea* species. Fig. 1 — *S. vallicola* Woodson, Allen 3541, palosclereids shown as they are seen through the upper epidermis of the cleared leaf and in transverse sections. Figs. 2, 3 — *S. bicolor* (Bentham) de Roon, Killip & Garcia 33206; Fig. 2: palosclereids seen through the upper epidermis; Fig. 3: sclereid from the spongy mesophyll. Fig. 4–6 — *S. exauriculata* Delp., Matuda 1853; Fig. 4: sclereids from the marginal region; Figs. 5, 6: sclereids from the spongy mesophyll. Fig. 7 — *S. dasystachya* Gilg, Schunke 20, sclereids from the spongy mesophyll near the midrib. Figs. 8–10 — *S. gilgii* Al. Richter, Woodson 1899, sclereids from the spongy mesophyll; Fig. 8: marosclereids from the marginal region; Fig. 9: irregularly shaped astrosclereid-like sclereids; Fig. 10: librosclereids.

PLATE III

Sclereids of *Souroubea guianensis* Aublet. Selection showing the great variation of form of sclereids within this species. Figs. 1–8 — rhizosclereids seen through the upper epidermis of cleared leaves showing the projections spreading under the epidermis. Figs. 9–13 — rhizosclereids seen in transverse sections. Figs. 14–16 — typical ophiurosclereids. Figs. 17–21 — transitions between ophiurosclereids and librosclereids. Figs. 22–25 — H-shaped librosclereids. Figs. 26–28 — typical librosclereids.

PLATE IV

Sclereids of *Ruyschia* and *Souroubea* species. The rhizosclereids from the palisade parenchyma are figured as seen through the upper epidermis of the cleared leaf, showing the projections underspreading the epidermis (Figs. 1–3, 16) and as seen in transverse sections (Figs. 4–6, 17). The other types are figured as seen in cleared leaves or in macerations. Figs. 1, 4, 7 — *R. pilophora* Tr. et Pl., von Schneidern s.n.; Figs. 1, 4: rhizosclereids; Fig. 7: astrosclereid. Figs. 2, 5 — *R. tremadena* (Ernst) Lundell, Steyermark 55105, rhizosclereids. Figs. 3, 6, 8 — *R. clusiaefolia* Jacq., Duss 278; Figs. 3, 6: rhizosclereids; Fig. 8: astrosclereid. Figs. 9, 14, 22 and 23 — *S. bicolor* (Bentham) de Roon, Killip & Garcia 33206, astro- and ophiurosclereids. Fig. 10 — *S. vallicola* Woodson, Allen 3541, astrosclereid. Figs. 11–13 — *S. pachyphylla* Gilg, Spruce 4469, Ule 6320, Williams 7013, astrosclereids and transitions towards ophiurosclereids. Fig. 15 — *S. didyma* (Wittm.) Gilg, Kanehira 198, astrosclereid. Figs. 16, 17, 24, 25 — *S. spec.*, Krukoff 11037, Gay 843; Figs. 16, 17: rhizosclereids; Figs. 24, 25: librosclereids. Figs. 18–21 — *S. peruviana* (Wittm.) Gilg, Mexica 8310, ophiurosclereids.

PLATE V

Sclereids of species of *Norantea* subg. *Marcgraviastrum*. The rhizosclereids are figured as seen through the upper epidermis of the cleared leaf, showing the projections underspreading the epidermis (Figs. 1–5, 15, 17) and as seen in transverse sections (Figs. 6–10, 16, 18). The other types from the spongy parenchyma are figured as they are seen intransverse sections or in macerations. Figs. 1, 6, 11 — *N. pardoana* Gilg, Uribe Uribe 1953; Figs. 1, 6: rhizosclereids; Fig. 11: astrosclereid. Figs. 3, 8, 13 — *N. brenesii* Gilg, Brenes 5570; Figs. 3, 8: rhizosclereids; Fig. 13: ophiurosclereid. Figs. 4, 9 — *N. brachystachya* (Rusby) de Roon, Williams 1461, rhizosclereids. Figs. 5, 10, 14, 24, 25, 28 — *N. weddelliana* Baillon, Bang 290; Figs. 5, 10: rhizosclereids; Fig. 14: astrosclereid; Fig. 24: ophiurosclereid; Fig. 25: librosclereid; Fig. 28: short librosclereid from the midrib region. Figs. 15, 16, 20 — *N. spec.*, Cuatrecasas 23618; Figs. 15, 16: rhizosclereids; Fig. 20: astrosclereid. Figs. 17–19, 21–23, 26, 27 — *N. macrocarpa* G. Don, Pavon s.n., Nuñez 704; Figs. 17, 18: rhizosclereids; Figs. 19, 21: transitional forms between astro- and ophiurosclereids; Figs. 23, 27: ophiurosclereids; Figs. 22, 26: librosclereids.

PLATE VI

Sclereids of species of *Norantea* subg. *Marcgraviastrum*. The rhizosclereids are figured as seen through the upper epidermis of the cleared leaf, showing the projections underspreading the epidermis (Figs. 1–9) and as seen in transverse sections (Figs.

10–14, 20–26). The other types from the spongy mesophyll are figured as seen in cleared leaves or in macerations. Figs. 1, 4, 10, 15, 27 — *N. sodiroi* Gilg; Acosta Solis 6153; Figs. 1, 4, 10: rhizosclereids; Fig. 15: astrosclereid; Fig. 27: librosclereid. Figs. 2, 5, 11, 16-19, 28-30 — *N. subsessilis* (Bentham) Donn. Smith, Killip & Garcia 33217; Figs. 2, 5, 11: rhizosclereids; Figs. 16: brachysclereids; Figs. 17-19: astro-ophiurosclereids; Figs. 28–30: librosclereids. Figs. 3, 6, 12, 20, 22, 36 — *N. pendula* Lanj. et v. Heerdt, B.W. 5682; Figs. 3, 6, 12: rhizosclereids; Fig. 20: rhizosclereid type 2; Fig. 22: rhizosclereid type 3; Fig. 36: librosclereid. Figs. 7–9, 13, 14, 21, 23, 33–35 — *N. spec.*, Schultes & Cabrera 14931; Figs. 7–9, 13, 14: rhizosclereids; Figs. 21, 23: rhizosclereids type 2; Figs. 33–35: librosclereids. Figs. 24–26, 31, 32 — *N. spec.*, Cuatrecasas 15456; Figs. 24–26: rhizosclereids; Figs. 31, 32: librosclereids. Fig. 37 — *N. spec.*, Killip & Cuatrecasas 39159, librosclereid.

PLATE VII

Sclereids of *Marcgravia* sect. *Plagiothalamium*. All the sclereids are figured as they are seen in transverse sections. Fig. 1 — *M. sororopaniana* Steyerm., Steyermark 60127, brachysclereid. Figs. 2–4 — *M. spec.*, Fagerlind & Wibom 1166B, brachysclereids and idiosclereid from the midrib region. Fig. 5 — *M. spec.*, Steyermark 75089, idiosclereid. Fig. 6 — *M. eichleriana* Wittm., Schultes & Cabrera 10105C, idiosclereid. Fig. 7 — *M. spec.*, Fanshawe & Maguire 23467, brachysclereid. Fig. 8 — *M. gentlei* Lundell, Gentle 3176, astrosclereids. Fig. 9 — *M. williamsii* Macbride, Cuatrecasas 11251, idiosclereid. Figs. 10–12 — *M. spec.*, Core 1545, idiosclereids from the midrib region. Figs. 13–14 — *M. coriacea* Vahl, Archer 7986, idiosclereids. Fig. 15 — *M. spec.*, Killip & Cuatrecasas 39100, idiosclereids. Fig. 16 — *M. spec.*, Fendler 2281, idiosclereid. Fig. 17 — *M. evenia* Kr. et Urb., Alain & Lopez 19646, idiosclereid. Figs. 18, 19 — *M. lineolata* Urb., Box 1941, idiosclereids.

PLATE VIII

Idiosclereids of species of *Marcgravia* sect. *Orthothalamium*. All the sclereids are figured as they are seen in transverse sections. Figs. 1, 2 — *M. angustifolia* Ruiz et Pavon apud López, Pavon s.n. Fig. 3 — *M. crenata* Poeppig ex Wittm., Poeppig 1477. Figs. 4, 5 — *M. magnibracteata* Lanj. et v. Heerdt, B.W. 4119. Figs. 6, 8, 9 — *M. mexicana* Gilg, Wawra 1132. Figs. 7, 10, 12 — *M. comosa* Presl, R.B. 48131. Figs. 11, 13 — *M. spec.*, Skutch 3762.

PLATE IX

Idiosclereids of species of *Marcgravia* sect. *Orthothalamium*. All the sclereids are figured as they are seen in transverse sections. Fig. 1 — *M. spec.*, Skutch 3762. Figs. 2, 3 — *M. macrophylla* (Wittm.) Gilg, Poeppig 2005. Figs. 4, 5 — *M. rectiflora* Tr. et Pl., Sintenis 269. Figs. 6, 7, 11 — *M. trinitatis* Presl, Duss 4629. Figs. 8–13 — *M. oblongifolia* Pavon ex Wittm., Ruiz 157. Fig. 14 — *M. flagellaris* Poeppig ex Wittm., Poeppig 2026.

PLATE X

Idiosclereidlike sclereids of species of *Marcgravia* sect. *Orthothalamium*. All the sclereids are figured as they are seen in transverse sections. They are all oriented more or less vertically and all, except those shown in Figs. 14 and 16, are touching the upper epidermis. Figs. 1–4, 16 — *M. spec.*, Cowan 38207. Fig. 5 — *M. spec.*, Mexia 7109. Figs. 7–9 — *M. leticiana* (Macbr.) de Roon, Krukoff 8491, Kuhlmann 1248. Figs. 10–15 — *M. flagellaris* Poeppig ex Wittm., Poeppig 2026, Ule 5635.

PLATE XI

Ophiurosclereid- and librosclereid-like sclereids from the spongy parenchyma of species of *Marcgravia* sect. *Orthothalamium*. All the sclereids are figured as they are seen in cleared leaves or in macerations. They are oriented parallel to the epidermis. Figs. 1, 2, 5–7 — *M. flagellaris* Poeppig ex Wittm., Poeppig 2026, Ule 5635. Figs. 3, 11 — *M. leticiana* (Macbr.) de Roon, Krukoff 8491, Kuhlmann 1248. Figs. 4, 10 — *M. spec.*, Mexia 7109. Fig. 8 — *M. spec.*, Aristeguieta 4460. Fig. 9 — *M. trinitatis* Presl, Duss 4629.

PLATE XII
Osteoclereids of species of *Marcgravia* sect. *Orthothalamium*. All the sclereids are figured as they are seen in transverse sections. Figs. 1, 4 — *M. brownei* (Tr. et Pl.) Kr. et Urb., Williams 10435, Killip 5577. Figs. 2, 3 — *M. goudotiana* (Tr. et Pl.) de Roon, Goudot s.n. Fig. 5 — *M. myriostigma* Tr. et Pl., Cuatrecasas 15597. Fig. 6 — *M. spec.*, Cuatrecasas 16890.

PLATE XIII
Morphological series showing the derivation of the types of sclereids from the palissade parenchyma (Fig. 1) and the spongy parenchyma (Fig. 2) in the genera *Ruyschia*, *Souroubea* and *Norantea*. Figs. 1A and B: palosclereids; C: rhizosclereid type 1; D: rhizosclereid type 2; E: rhizosclereid type 3. Figs. 2A: brachysclereid; B: idiosclereid; C: astrosclereid; D: ophiurosclereid; E: librosclereid.

PLATE XIV
Transverse sections through the leaves of *Marcgravia* species showing the sclereid pattern. Semidiagrammatic. Fig. 1 — *M. mexicana* Gilg. Fig. 2 — *M. magnibracteata* Lanj. et v. Heerdt. Fig. 3 — *M. leticiana* (Macbr.) de Roon. Fig. 4 — *M. spec.*, Aristeguieta 4460. Fig. 5 — *M. brownei* (Tr. et Pl.) Kr. et Urb.

PLATE XV
Transverse sections through leaves of *Marcgravia* and *Souroubea* species showing the sclereid pattern. Semidiagrammatic. Fig. 1 — *M. gentlei* Lundell. Fig. 2 — *M. coriacea* Vahl. Fig. 3 — *S. guianensis* Aubl. Fig. 4 — *S. vallicola* Woodson.

PLATE XVI
Transverse sections through leaves of *Norantea* species showing the sclereid pattern. Semidiagrammatic. Fig. 1 — *N. peduncularis* Poeppig ex Wittm. Fig. 2 — *N. sodiroi* Gilg. Fig. 3 — *N. weddelliana* Baillon.

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THE TAXONOMIC SIGNIFICANCE OF TWO ARTIFICIALLY PRODUCED HYBRIDS IN THE GENUS CAMPANULA

TH. W. J. GADELLA

(*Botanical Museum and Herbarium, Utrecht*)

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Abstract

Artificial hybridization experiments were carried out between two species-pairs in the genus *Campanula*, viz. between *C. persicifolia* and *C. latiloba*, and between *C. alliariifolia* and *C. ochroleuca*. The hybrid between *C. persicifolia* and *C. latiloba* is completely sterile. For this reason the treatment as separate species of these closely allied taxa is justified. The hybrid between *C. alliariifolia* and *C. ochroleuca*. on the other hand, is completely fertile. Therefore, it is advisable to regard *C, ochroleuca* and *C. alliariifolia* as conspecific, as was previously done by Kem. Nathadze.

Introduction

In a previous paper (Gadella, 1964) the results of crossing experiments between species belonging to several groups of the genus *Campanula* have been described. Valuable information on the delimitation of infrageneric natural species groups could be obtained. But hybridization experiments may also support the separation of taxa which are closely allied morphologically, or, on the other hand, may indicate that such taxa could better be treated as conspecific.

An example of the first possibility is presented by *C. persicifolia* and *C. latiloba*, of the latter by *C. alliariifolia* and *C. ochroleuca*. In this paper a description of the produced hybrids will be given, as well as a discussion of their taxonomic significance.

Material and methods

The plants were grown from seeds, which were obtained from the following sources:

C. alliariifolia Willd., Coll. No. C 36, Botanical Garden of Siena

C. ochroleuca (Kem. Nath.) Kem. Nath., Coll. No. C 289, Botanical Garden of Jena

C. latiloba DC., Coll. No. C 487, Botanical Garden of Oxford

C. persicifolia L., Coll. No. C 542, collected in nature, near Klagenfurt, Austria.

For the methods of emasculation and pollination, see Gadella, 1964, p. 63. The flowers were emasculated in all cases, despite the fact that artificial self-pollination did not result in the formation of mature seeds. In previous papers (Gadella, 1963, 1964) it could be shown that most of the species of the genus *Campanula* are highly allogamous. However, in the summer of 1964 some seeds could be obtained after selfpollination in some strains of *C. rotundifolia*, whereas in most other strains no seed-formation could be demonstrated.

H. Bielawska (1964) considers *C. rotundifolia* to be selffertile to a very limited extend. In the opinion of Podlech (1965) at least most of the species of the subsection *Heterophylla* are highly allogamous, only in the species *C. baumgartenii* subsp. *baumgartenii* the formation of ripe seeds could be observed when cross pollination failed to occur. According to Damboldt (1965a) most of the species of the *Isophyllae* are selfsterile, with the exception of *C. garganica*. Therefore, Damboldt (1965a, b) is of the opinion that it is not necessary to emasculate the flowers of most species. Bielawska (in litt.) obtained seeds in the species *C. rotundifolia* after selfpollination, after some years of negative results. She is of the opinion that the weather conditions and the season of pollination may be important factors. At any rate, attention should be paid to the possibility of very restricted selffertility, and therefore it seems better, in my opinion, to emasculate the flowers. Voucher specimens of the hybrids and of the parental species have been deposited in the herbarium of the State University of Utrecht.

Results

1. **Campanula persicifolia** L. (♀) X **Campanula latiloba** DC. (♂)

These species belong to the small group of species of the genus *Campanula* which is characterized by the following combination of cytological and morphological characters:
Long chromosomes (4–6 μ), $2n=16$; Basal leaves lanceolate, branches of the stigma equalling the glabrous style, capsule 3-locular, erect, dehiscing near the apex.

The two species are closely allied. The differences between the species as well as the characters of the hybrid are shown in table 1. (all measurements pertain to plants after some years of experimental cultivation under the same conditions).
7 flowers of *C. persicifolia* were emasculated and pollinated with pollengrains of *C. latiloba*. The capsules of 3 flowers contained many seeds after some weeks. 31 seedlings were obtained and grown in pots in the open. The hybrids grew vigorously in their first year, but became yellowish in the spring of their second year. Despite this fact, the plants began to flower in the second half of June. All plants proved to be highly sterile. No seeds were formed, whereas an examination of the young anthers revealed the fact that only a very few shrivelled and abnormal as well as micro-pollengrains had been formed. Only a few pollenmothercells could be observed. Univalents and multivalents and the formation of bridges were found in many cases. The tapetum-cells proved to be very large.

TABLE 1

A comparison of the characters of *Campanula persicifolia* and *Campanula latiloba* and their hybrid. The dimensions of all parts of the plants of *C. persicifolia* are much larger under cultivation than of the same plants growing in the wild

Characters	**C. persicifolia**	**Hybrid**	**C. latiloba**
Height of the stem	up to 100 cm	up to 45 cm	up to 60 cm
Diameter of the stem base	up to 4 mm	up to 3 mm	up to 8 mm
Cauline leaves	upper stemleaves much shorter than the basal ones	upper stemleaves scarcely shorter than the basal ones	upper stemleaves scarcely shorter than the basal ones
Margin of the basal leaves	remotely crenulate-dentate	rather densely dentate	rather densely dentate
Length of the pedicel	50 (30–70) mm	30 (20–30) mm	1 (1–2) mm
Length of the petals	35 (34–36) mm	20 mm	22–24 mm
Length of the sepals	16 (15–17) mm	12 (11–12) mm	11 mm
Shape of the corolla	deeply campanulate	rather shallowly campanulate	very shallowly campanulate
Depth of the corolla	25 mm	13 mm	16 mm
Diameter of the corolla	35 mm	20 mm	20–25 mm
Diploid number of chromosomes	16	16	16

2. **Campanula alliariifolia** Willd. (♀) × **Campanula ochroleuca** (Kem. Nath.) Kem. Nath. (♂)

The species *C. alliariifolia* and *C. ochroleuca* belong to the subsection *Cordifoliae* (Fom.) Fed. in the system of FEDOROV (1957). They belong to the large group of species of the genus *Campanula* which is characterized by the following combination of morphological and cytological characters: Short chromosomes, 1,5–3 μ, mostly ca. 2 μ, $2n = 34$; Calyx appendages between the calyx-lobes, style 5–10 × longer than the branches of the stigma, capsule 3-locular, mostly dehiscing basally with 3 valves.

The two species are very closely allied. The differences between the parental species as well as the characters of the hybrid are given in table 2. (all measurements refer to plants after several years of cultivation under the same conditions).

7 flowers of *C. alliariifolia* were emasculated and pollinated with pollengrains of *C. ochroleuca.* All capsules contained mature seeds. 23 seedlings were maintained. The seedlings grew vigorously and did not become yellowish in their first or second year, as was the case with most other artificially produced hybrids in the genus *Campanula.* The plants produced many flowers in the second year and proved to be fully fertile, each capsule containing many mature seeds.

DISCUSSION

The species *C. persicifolia* and *C. latiloba* are allopatric. *C. latiloba* occurs in Asia Minor (Bithynia), whereas *C. persicifolia* inhabits Europe (N., W. and C.) and Siberia. The taxa are capable of limited gene-exchange, as may be concluded from the above-mentioned experiments. BOISSIER (1875) remarks that in Macedonia and Thessalia (where the species is very rare according to CONTANDRIOPOULOS, 1964) some plants of *C. persifolia* have very short peduncles, thus approaching to *C. latiloba* in this respect. It seems desirable, in my opinion, to include these plants in a future crossing-program. For the moment it is justified to treat *C. persicifolia* and *C. latiloba* as separate species.

According to FEDOROV (1957) *C. alliariifolia* occurs in the Balcan Peninsula and in the Caucasus (W. and E. Cis-Caucasia; W.E. and S. Trans-Caucasia), whereas *C. ochroleuca* is endemic in the Cis-Caucasian area. *C. alliariifolia* occurs on rocks in the wood-zone and prefers limestone, *C. ochroleuca* occurs on rocks in the upper wood-zone and the subalpine-zone. The taxa are partially sympatric, but seem to be different in their ecological requirements. From Fedorov's treatment in the Flora U.S.S.R. it could be derived that in 1938 Kemularia Nathadze referred the plants with ochreous flowers to *C. alliariifolia*: *C. alliariifolia* Willd. subsp. *ochroleuca* Kem. Nath. Later, in 1949, the same author raised this taxon to specific rank: *C. ochroleuca* (Kem. Nath.) Kem. Nath. At least under garden conditions the two taxa are fully interfertile; there is no limitation

TABLE 2

A comparison of the characters of the species *Campanula alliariifolia* and *Campanula ochroleuca* and their hybrid

Characters	**C. alliariifolia**	**hybrid**	**C. ochroleuca**
Length of the stem	55 (40–60) cm	50 (45–65) cm	40 (30–45) cm
Apex of the basal leaves	mostly obtuse	mostly acute	mostly acute
Length of the basal leaves	70 (40–110) mm	55 (50–65) mm	50 (40–60) mm
Length of the petiole of the basal leaves	14 (10–17) cm	14 (12–15) cm	9 (8–10) cm
Branches of the main stem	if branched, branches much shorter than the main stem	branches of intermediate length	if branched, branches scarcely shorter than the main stem
Shape of the inflorescence	long, one-sided raceme	long, one-sided raceme	not strictly one-sided, lax raceme
Length of the leaves of the inflorescence	very short, much shorter than the stem leaves	very short	gradually diminishing, not much shorter than the upper stem-leaves
Colour of the corolla	white (yellow when dry)	very light yellowish-white	ochreous
Shape of the corolla	campanulate, more or less inflated	campanulate, not inflated	narrowly tubular
Ratio length calyx: length corolla	1 (:) 4–5	1 (:) 3	1 (:) 3
Ratio length calyx: width calyx	2 (:) 1	2 (:) 1	3–4 (:) 1
Diploid chromosome number	34	34	34

to gene-exchange. For this reason it is justified to consider *C. alliariifolia* and *C. ochroleuca* to be conspecific. The differences in ecological preference and the morphological differences support the treatment of *C. ochroleuca* as a subspecies of *C. alliariifolia*.

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PHYTOGEOGRAPHICAL RELATIONS IN THE NORTH WEST EUROPEAN HEATH

J. T. DE SMIDT

(*Botanical Museum and Herbarium, Utrecht*)

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1. Introduction

The water economy, the mineral content of the soil, and human influence are the principal ecological factors governing the variation of the heath vegetation of a limited region. Sloping of the surface is also an important factor. In hilly country it is of a twofold nature: on the one hand the difference between high and low altitudes, based on the water economy, on the other hand differences in (micro-) climate. If the hills are higher, this results in greater climatic differences. In extremely oceanic and in boreal regions a rise in altitude of 100 m is sufficient for creating a noticeable decrease in temperature and an increase in precipitation, aerial moisture, and wind force. This results in the occurrence on the hills of heath communities that have their main distribution more to the North. The same observation was made by Gimingham (1961). On Slieve League on the Donegal coast (Ireland) *Salix herbacea* and *Lycopodium selago* occur in the heath at an altitude of 600 m, near Tongue on the Scottish north coast *Dryas octopetala*, *Saxifraga oppositifolia*, *Alchemilla alpina* and *Thalictrum alpinum* at an altitude of 60 m. West of Apeldoorn in the Netherlands are found extensive stretches of heath with abundant *Vaccinium myrtillus* and *V. vitis-idaea* at an elevation of 60–80 m, even on south-facing slopes. This is an area with high precipitation due to ascending air west of the hill ridge of the Eastern-Veluwe. Here the *Vacciniums*, elsewhere requiring the protection of the forest, can tolerate the habitat of the open heath (Stoutjesdijk, 1959; De Smidt, 1966). Higher elevation combined with north-facing slopes creates extreme conditions e.g. on Roc Trévézel (300–360 m) in Brittany, with *Vaccinium myrtillus*, *Melampyrum pratense*, *Hymenophyllum wilsonii* and *Rhytidiadelphus loreus*. These species are virtually lacking in the surrounding plains where the heath consists of such South Atlantic species as *Erica cinerea*, *E. ciliaris*, *Ulex gallii*, *Lobelia urens*, *Lithospermum prostratum* and *Symethis planifolia*.

Conversely, in protected valleys and on richer soil we find more southerly communities to the North of their main area. In the Maas valley between Maaseik and Maastricht a type of löss, rich in minerals and with a mild local climate supports a type of *Calluna* vegetation 1.50 m high with as co-dominant species *Sarothamnus scoparius*. This is a subatlantic community with Southern and Central European tendencies, mainly developed in low mountains: Eifel, Black Forest, and in a modified composition on the Plateau Central (De Smidt, 1966). Often it is the interaction between local climate and soil conditions that provides a suitable habitat for such "extra-zonal" communities, as is the case with this *Calluna-Sarothamnus* heath. On Roc Trévézel the local climate is the main factor. An "extra-zonal" heath due to soil conditions is the poor *Calluna* heath with *Hypnum cupressiforme var. ericetorum*, *Festuca ovina*, *Carex pilulifera* on deep sandy deposits at Revingehed, East of Lund (South Sweden). This type is common in Northern Belgium, the Netherlands, and Northwest Germany with its northern border in South Jutland. A striking phenomenon is the absence of boreal species that are common in the heath of the region: *Vaccinium myrtillus*, *V. vitis-idaea*, *Cornus suecica*, *Trientalis europaea*, *Lycopodium clavatum*.

This paper chiefly deals with the phytogeographical characteristics of the "zonal" heaths. This term is employed for the main types in the Western European heath vegetation that can be distinguished on the basis of phytogeographical spectra. The criterium for delimiting geographically these main vegetation types is the presence of a group of species with a similar distribution. Since the distribution of the species is chiefly due to climatic factors, the area of the main vegetation types, too, depends chiefly on the macro-climate.

Böcher (1943) was the first to employ spectra of distribution types for classifying the European heathvegetations. Schubert (1960) also suggested a classification mainly based upon phytogeographic characters. Gimingham (1961), too, made some phytogeographical conclusions in his study on the variation of floristic composition and quantitative estimates of cover in the North European heath communities.

2. The distribution of the species in the north west european heaths

In Tables 1–4 are listed the total number of 384 species which have been recorded by the author in the North West European heath. In each separate column all those species are enumerated which were recorded in a certain part of Western Europe. Initially smaller areas had been listed separately, but several could be combined because of their great similarity. This was the case with Scotland and Wales, and with the Northern Netherlands, Northwest Germany, and Southern Jutland.

The following distribution types are distinguished in the tables.

a. widely distributed
b. subatlantic
c. atlantic
d. mediterranean atl.
e. eu-atlantic
f. boreal-atlantic
g. boreal-montane
h. arctic-alpine
i. central-meridional
j. continental

The overall species list can be subdivided into four groups.

TABLE 1. Species widely distributed in the North-West European heath

Distribution type	Region no. *)	1	2	3	4	5	6	7	8	9	10
a.	Calluna vulgaris	x	x	x	x	x	x	x	x	x	x
	Festuca ovina	x	x	x	x	x	x	x	x	x	x
	Molinia caerulea	x	x	x	x	x	x	x	x	x	x
	Hypnum cupr. v. ericetorum	x	x	x	x	x	x	x	x	x	x
	Pleurozium schreberi	x	x	x	x	x	x	x	x	x	x
	Dicranum scoparium	x	x	x	x	x	x	x	x	x	x
	Polytrichum commune	x	x	x	x	x	x	x	x	x	x
	Aulacomnium palustre	x	x	x	x	x	x	x	x	x	x
	Cladonia uncialis	x	x	x	x	x	x	x	x	x	x
	– gracilis	x	x	x	x	x	x	x	x	x	x
	– pyx. v. chlorophaea	x	x	x	x	x	x	x	x	x	x
	– sylvatica	x		x	x	x		x	x	x	x
	– crispata	x	x	x	x	x	x	x	x	x	
	– furcata	x	x	x	x	x	x	x	x	x	
	– squamosa	x			x	x	x	x	x	x	x
	– cocc. v. pleurota	x	x		x		x	x	x	x	x
	– floerkeana	x	x	x	x	x	x	x	x	x	
	– verticillata	x	x		x	x	x	x			x
	– cornutoradiata	x			x		x	x	x	x	x
	– rangiformis	x		x	x			x	x	x	x
	– macilenta	x			x		x	x		x	
	– pityrea		x		x		x	x	x	x	
	Parmelia physodes	x	x		x	x	x	x	x	x	x
	Cornicularia aculeata	x	x		x	x	x	x	x	x	x
	Peltigera canina			x	x	x		x	x	x	
	Leucobryum glaucum	x	x	x	x	x	x	x		x	x
	Polytrichum piliferum	x	x		x	x	x	x	x		x
	Polytrichum juniperinum	x			x			x	x		x
	Scleropodium purum	x	x	x	x	x		x	x	x	
	Sphagnum molluscum	x	x	x	x	x	x	x	x	x	
	– compactum	x	x	x	x	x	x	x		x	x
	– papillosum	x	x	x	x	x	x			x	x
	– plumulosum	x		x	x			x		x	
	Lophocolea bidentata	x		x	x	x		x	x	x	
	Ptilidium ciliare		x	x	x	x	x	x	x	x	x
	Cephaloziella sp.		x	x	x		x	x		x	
	Orchis mac. ssp. ericetorium	x	x	x	x	x	x	x	x	x	
	Succisa pratensis	x	x	x	x	x		x	x	x	
	Viola riviniana	x	x		x	x		x	x	x	
	Carex nigra		x	x	x	x		x	x	x	
	Salix repens	x	x		x	x	x	x	x	x	x
	Agrostis tenuis	x	x	x	x	x		x	x	x	x
	– canina		x	x	x	x	x	x	x	x	x
	– stolonifera	x	x	x	x	x		x		x	
	Solidago virgaurea	x	x	x	x	x		x		x	x
	Thymus serpyllum		x	x	x			x	x	x	x
	Lotus corniculatus	x	x	x	x	x			x	x	
	Juniperus communis	x			x	x		x	x	x	x
	Rumex acetosella	x	x		x			x		x	x
	Scapania nemorosa	x		x	x	x		x		x	
	Plantago lanceolata	x	x	x	x	x			x	x	x
	Rumex acetosa	x			x				x	x	x
	Prunella vulgaris		x	x	x	x			x	x	

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*) For explanation of region no's see Table 5, p. 643.

TABLE 1 (*continued*)

Distribution type	Region no.	1	2	3	4	5	6	7	8	9	10
	Linum catharticum	x		x	x					x	
	Sphagnum acutifolium		x	x	x	x			x	x	x
	Rhytidiadelphus squarrosus		x	x	x					x	x
	Polytrichum strictum			x	x	x				x	
	Hieracium pilosella			x	x	x	x	x	x	x	x
	Campanula rotundifolia			x	x	x		x	x	x	x
	Luzula multiflora		x	x	x	x		x	x	x	
	Sorbus aucuparia			x	x	x		x		x	
	Gymnocolea inflata		x		x	x	x	x	x	x	
	Cladonia destricta	x						x	x	x	
	Festuca rubra	x	x	x	x		x	x	x	x	x
	Holcus lanatus	x		x	x			x	x	x	
	Achillea millefolium	x				x			x	x	x
	Frangula alnus	x	x			x		x		x	
	Quercus robur	x	x				x	x	x	x	
	Anthoxanthum odoratum		x	x	x	x		x	x	x	
	Mnium hornum			x	x	x		x			
	Antennaria dioica		x		x	x		x	x	x	
	Poa pratensis		x		x				x		
	Genista tinctoria	x						x	x		
	Cetraria glauca	x		x	x	x		x	x	x	
	Cladonia glauca	x	x		x		x	x		x	x
	Barbilophozia barbata				x	x		x	x	x	
	Hylocomium splendens	x	x	x	x	x		x	x	x	x
	Veronica officinalis		x		x	x			x	x	x
	Platanthera bifolia	x		x				x	x	x	x
	Hieracium umbellatum	x				x	x	x	x	x	x
b.	Galium saxatile	x	x	x	x	x	x	x	x	x	x
	Potentilla erecta	x	x	x	x	x	x	x	x	x	x
	Carex pilulifera	x	x	x	x	x	x	x	x	x	x
	Carex panicea	x	x	x	x	x	x	x	x	x	x
	Nardus stricta	x	x	x	x	x	x	x	x	x	x
	Sieglingia decumbens	x	x	x	x	x	x	x	x	x	x
	Cladonia impexa	x	x	x	x	x	x	x	x	x	x
	Drosera intermedia	x	x	x				x	x	x	
	Pedicularis sylvatica	x	x	x	x	x	x	x	x	x	
	Hypochoeris radicata	x	x	x	x		x	x	x	x	x
	Euphrasia micrantha		x	x	x				x	x	
	Carex echinata			x	x	x			x	x	
	Viola canina	x	x			x		x	x	x	
	Luzula campestris		x	x	x	x		x	x	x	x
	Oxalis acetosella	x		x	x	x			x	x	
	Anthyllis vulneraria	x	x						x		
	Deschampsia flexuosa			x	x	x	x	x	x	x	x
	Polygala serpyllifolia	x	x	x	x	x	x	x	x		
	Gentiana pneumonanthe	x	x				x	x	x		
	Cuscuta epithymum	x	x				x	x			
	Lonicera periclymenum	x	x	x	x			x	x	x	
	Diplophyllum albicans	x		x	x	x		x	x	x	
	Frullania tamarisci	x		x	x	x			x	x	
	Sarothamnus scoparius	x			x		x	x	x		
	Carex pulicaris	x	x		x	x		x	x		
	Lophozia ventricosa	x		x	x	x	x	x	x		
	Calypogeia trichomanes		x	x	x		x	x	x		

TABLE 1 (*continued*)

Distribution type	Region no.	1	2	3	4	5	6	7	8	9	10
	Odontoschisma sphagni	x	x	x	x	x	x	x			
	Orthocaulis attenuatus	x		x		x		x			
c.	Narthecium ossifragum	x	x	x	x	x	x	x	x	x	
	Juncus squarrosus		x	x	x	x	x	x	x	x	
	Erica tetralix	x	x	x	x	x	x	x	x	x	
	Myrica gale	x		x	x	x	x	x	x	x	
	Silene maritima	x				x				x	
	Rosa pimpinellifolia	x			x	x		x	x		
	Genista anglica	x	x		x		x	x	x		
	Campylopus flexuosus	x	x	x			x	x			
f.	Scirpus caespitosus	x	x	x	x	x	x	x	x	x	
g.	Vaccinium myrtillus	x		x	x	x	x	x	x	x	x
	,, vitis-idaea			x	x	x		x	x	x	x
	,, oxycoccus			x	x		x	x	x	x	
	Arctostaphylos uva-ursi			x	x	x		x	x	x	
	Empetrum nigrum	x		x	x	x		x	x	x	x
	Pinus sylvestris		x		x	x	x	x		x	
	Betula pubescens				x	x	x	x		x	
	,, verrucosa		x		x	x	x	x		x	
	Populus tremula		x			x			x	x	
	Rhynchospora alba	x	x	x				x			
	Eriophorum angustifolium	x	x	x	x		x	x	x	x	
	,, vaginatum		x	x	x		x	x	x		
	Drosera rotundifolia	x	x	x	x	x	x	x	x	x	
	Melampyrum pratense	x		x	x	x	x	x	x	x	
i.	Jasione montana	x		x	x			x	x		x
	Armeria maritima	x			x	x			x	x	x
	Filipendula hexapetala	x	x							x	
	Rhacomitrium canescens	x								x	

2.1. *Species widely distributed in the heath* Table 1

These species occur in all ten areas or, if in less, then without clear preference for certain ones among them. To this group belong 138 species, more than one third of the total number recorded in the heath. Nearly 60 % of them are not only widely distributed in the North West European heath, but also in the rest of Europe and Asia, and often as well in North America. More than 20% have a subatlantic area; this is much more than in the three other groups. This shows that the widely distributed type and the subatlantic type form the connecting element in the heath formation of the North West European plains. Besides there are smaller numbers of the boreal-montane (10%) and the atlantic (6%) distribution type. It is clear that in this group we do not find any species with pronouncedly mediterranean, arctic- alpine, continental or extremely atlantic distribution, the area under consideration being situated in the atlantic and subatlantic region from Southern Scandinavia to Central France and from Ireland to North Germany. Less obvious is the scarcity of species with Central or South European tendencies. Among the four species placed in this category two, viz. *Jasione montana* and *Armeria maritima*, are polymorphic and comprise oceanic forms: *Jasione montana ssp. maritima* in the coastel heath of Ireland and Brittany and the coastal form of *Armeria maritima* in Brittany, Scotland, and Southern Scandinavia.

A striking phenomenon is the rather high percentage of the boreal-montane element (10%). It consists partly of trees of the boreal-montane woods, *Pinus*, *Betula* and *Populus tremula*, that reach rather far South in Central and Western Europe on poor soils in the plains. A few species that form part of these woods in the undergrowth, *Vaccinium myrtillus*, and *V. vitis-idaea*, and *Melampyrum pratense*, also occur in the heath. As they penetrate more southerly regions, they are more strictly confined to the cool and moist microclimate of the woods. In Scandinavia and Scotland the macroclimate permits their frequent occurrence in the open heath, outside the protecting woods. In the heath of Northern Germany and southward they are confined to north-facing slopes and to hilly country with a cool moist micro- resp. local climate. The rest of the boreal-montane species of this group are plants of peat bogs except *Arctostaphylos uva-ursi.* In the oligotrophic peat bogs and boggy heaths of the Dutch and German lowland, of Brittany and the British Isles they find a suitable habitat far to the South of their main area. BÖCHER (1943) calls the distribution of *Arctostaphylos uva-ursi* very problematic, as it is frequent both in extremely oceanic regions (Western Norway, Scotland, Northern Ireland) and in rather continental areas in the northern part of Central Europe. As a possible explanation Böcher suggests the existence of different biotypes originating from populations that survived the glaciation under different climatic conditions.

2.2. *Species with preference for northern heaths* Table 2. Scotland, Western Norway, Southern Sweden, Northern Jutland.

Widely distributed, atlantic and subatlantic species are reduced to half the percentage in the preceding group. In the other hand the portion of boreal-montane species is more than twice as high. The boreal-atlantic element is also strong: 12 out of 15 species with this type of distribution occurring in the North West European heath belong to this group. The arctic-alpine element is, however, lacking as it is confined to group C, Table 3: species with a more westerly distribution in the heath. Apart from the boreal flora element it is the continental element (17%) that particularly characterises this group; it is virtually absent from the others. Within the group of northern heathland species a shift in the flora elements may be observed as one moves eastward.

In Scotland the boreal-montane element (Table 3, g) comprises

TABLE 2. Species with preference for northern heaths

Distribution type	Region no.	1	2	3	4	5	6	7	8	9	10
a.	Epilobium angustifolium				x			x	x		
	Rhytidiadelphus triquetrus				x			x	x	x	
	Bazzania trilobata					x		x		x	
	Lophozia bicrenata						x	x			
	Ranunculus acer				x	x				x	
	Dicranum polysetum			x	x	x	x	x	x	x	x
	– spurium				x	x	x	x	x	x	x
	Pohlia nutans		x		x		x	x	x	x	x
	Galium verum								x	x	x
	Polygala vulgaris		x				x		x	x	x
	Fragaria vesca				x				x	x	x
	Lophocolea heterophylla						x	x		x	x
	Hieracium laevigatum							x		x	x
	Vicia cracca								x	x	
	Stellaria graminea								x	x	x
	Trifolium repens								x	x	x
	Silene cucubalus								x		x
	Hypericum perforatum									x	x
	Plagiothecium denticulatum								x	x	x
	Orthocaulis lycopodioides							x			x
	Hypericum maculatum									x	
	Silene nutans									x	
	Briza media									x	
	Trifolium arvense										x
	Knautia arvensis										x
	Erigeron acris										x
	Centaurea scabiosa										x
	Medicago falcata										x
b.	Veronica chamaedrys								x	x	x
	Genista pilosa						x	x	x	x	
	Juncus balticus								x		
	Lycopodium inundatum							x	x		
	Rosa tomentosa									x	
	Sedum telephium									x	
	Scleranthus perennis										x
	Ononis spinosa										x
	Ornithopus perpusillus										x
c.	Potentilla anglica									x	
	Carex trinervis									x	
	– arenaria			x	x			x	x	x	x
f.	Pinguicula vulgaris				x	x			x	x	
	Anemone nemorosa				x	x			x	x	
	Luzula pilosa				x	x			x	x	
	Cornus suecica					x			x	x	
	Convallaria majalis					x				x	
	Ajuga pyramidalis					x				x	
	Rhynchospora fusca						x	x		x	
	Sorbus hybrida					x					x
	Lathyrus montanus			x	x				x	x	x
	Leucorchis albida								x	x	
	Ligusticum scoticum								x		

Table 2 (*continued*)

Distribution type	Region no.	1	2	3	4	5	6	7	8	9	10
g.	Lycopodium clavatum				x	x		x	x	x	x
	Cetraria islandica				x			x	x	x	x
	Majanthemum bifolium					x	x	x	x	x	
	Polypodium vulgare	x			x			x	x	x	x
	Trientalis europaea				x	x		x	x	x	
	Vaccinium uliginosum					x		x	x	x	x
	Cladonia rangiferina			x	x	x			x	x	x
	Dryopteris spinulosa				x			x	x	x	
	– linnaeana				x	x				x	
	– phegopteris					x				x	
	Galium boreale				x					x	
	Lycopodium annotinum					x				x	
	Equisetum sylvaticum					x				x	
	Sphaerophorus globosus				x				x		
	Evernia prunastri							x	x		
	Andromeda polifolia						x	x	x		
	Cladonia bellidiflora					x					
	Orthocaulis kunzeanus							x			
	Cladonia alpestris									x	
	Cetraria juniperina									x	
	Splachnum ampullaceum									x	
i.	Leontodon autumnalis				x	x			x	x	
	Carex montana								x	x	
	Rosa dumetorum									x	
	Saxifraga tridactylites									x	
	Melica nutans									x	
	Polygonatum odoratum									x	
	Dianthus deltoides										x
j.	Scorzonera humilis	x						x	x	x	
	Arnica montana							x	x	x	
	Hypochoeris maculata							x	x	x	
	Trifolium medium									x	
	Carex ericetorum								x	x	
	Pimpinella saxifraga								x	x	x
	Anemone pulsatilla								x	x	x
	Vicia cassubica									x	x
	Viscaria vulgaris									x	x
	Helictotrichon pratensis									x	x
	Prunus spinosa	x								x	x
	Cladonia mitis								x	x	x
	Genista germanica								x		
	Carex caryophyllea									x	
	Artemisia campestris										x
	Helichrysum arenarium										x

approximately as many species as in most parts of Scandinavia. The representation of the other flora elements is, however, much weaker, as calculated from the species that have a northern distribution in the heath. Instead, Scotland possesses some arctic-alpine, eu-atlantic, and a few mediterranean-atlantic species (see Table 3).

Western Norway has more boreal-atlantic species in the heath than Scotland, but in terms of the other elements it has more in common with the last named country than with the rest of Scandinavia. Floristically speaking too, the Western Norwegian heath is closer to the British than to the Scandinavian type. See especially Table 3 which lists some typically western species from Western Norway: *Erica cinerea*, *Hypericum pulchrum*, *Carex binervis*, *Juniperus nana*, *Blechnum spicant*, *Mylia taylori*, *Bazzania tricrenata*, *Anastrepta orcadensis*, *Breutelia chrysocoma*, *Campylopus atrovirens*.

Eastward the continental element is first encountered in the Dutch-German plain. It increases in North Jutland and reaches its peak in the region under study in South East Sweden (9 %). The same is true for the central-southern European species. BÖCHER (1943) lists the same species from the Eastern Danish heaths and SCHUBERT (1960) from the Central European heaths. The most widespread continental species are: *Pimpinella saxifraga*, *Scorzonera humilis*, *Arnica montana*, *Hypochoeris maculata*, *Carex ericetorum*, *Anemone pulsatilla* and *Cladonia mitis*. The presence of *Scorzonera humilis* in the Breton heath is a phytogeographical and ecological enigma. This species is common in Central Europe where it shows a predilection for mineral rich, dry, and often warm habitats. It decreases in general toward the atlantic side, except in Brittany where it reaches a second optimum. Contrary to what may be expected it does not occur in the driest habitats, but in very boggy heath. Probably it belongs to a different ecotype than the Central European plant.

2.3. *Species with preference for western heaths* Table 3

As far as heath is concerned these species have their optimum in Northern Ireland, Wales, Scotland and Western Norway. Characteristic is the optimal representation in the heath of the eu-atlantic and the arctic-alpine flora element. Of the 27 recorded eu-atlantic heathland species 23 belong to the present group. The four other species show preference for the south-atlantic heath of Southern Ireland and Brittany. The western heath shares a relatively high percentage of boreal-montane species (20 %) with the northern heath (22 %).

The arctic-alpine species are confined to this group. It mainly comprises species descending to sea-level on the North coast of Scotland (*Saxifraga oppositifolia*, *Thalictrum alpinum*, *Dryas octopetala*, *Alchemilla alpina*), or at least to low altitudes (*Empetrum hermaphroditum*, *Lycopodium alpinum*). *Salix herbacea* was met with in the heath of the Irish North West coast and *Juncus trifidus* on the West coast of Norway. The habitats are always exposed to strong wind and face the sea directly. The strong, almost continuously blowing wind is probably the most important factor governing the presence of these species. In combination with the mostly high atmospheric humidity and the low summer temperatures an environment is created that shows certain similarities to mountain conditions.

TABLE 3. Species with preference for western heaths

Distribution type	Region no.	1	2	3	4	5	6	7	8	9	10
a.	Cladonia strepsilis	x				x		x			
	Telaranea setacea	x	x	x	x		x	x			
	Cephalozia bicuspidata			x				x			
	Mylia anomala	x	x		x		x	x			
	Lepidozia reptans	x		x	x	x					
	Thuidium tamariscinum	x		x	x	x					
	Brachypodium pinnatum	x			x						
	Pteridium aquilinum ssp. aq.	x	x	x	x	x	x				
	Rhinanthus minor					x					
	Sphagnum rubellum	x		x	x						
	– recurvum		x	x	x						
	– cuspidatum			x		x					
b.	Schoenus nigricans	x	x	x	x						
	Cladonia papillaria	x			x						
	– degenerans	x			x						
	Juncus acutiflorus	x	x	x	x		x				
	Hedera helix				x						
	Lysimachia nemorum				x						
	Aquilegia vulgaris					x					
c.	Cirsium dissectum	x	x	x	x						
	Scapania gracilis	x		x	x						
	Digitalis purpurea	x			x						
	Ilex aquifolia			x	x						
	Blechnum spicant	x	x	x	x	x					
	Rhytidiadelphus loreus	x	x	x	x	x					
	Dicranum majus	x		x	x	x					
	Plagiothecium undulatum	x		x	x	x					
	Rhacomitrium lanuginosum	x		x	x	x					
	Campylopus brevipilus	x	x	x	x	x					
	Plantago maritima	x	x	x	x	x					
d.	Ulex galli	x	x	x	x						
	Pinguicula lusitanica	x		x	x						
	Teucrium scorodonia	x		x	x						
	Luzula maxima	x		x	x						
	Endymion nutans	x			x						
	Lejeunea cavifolia			x	x						
e.	Hymenophyllum wilsonii	x		x	x						
	Thymus drucei	x			x						
	Plagiochila spinulosa	x		x	x						
	Pleurozia purpurea			x	x						
	Herberta hutchinsiae			x	x						
	Mylia taylori			x	x	x					
	Bazzania tricrenata			x	x	x					
	Anastrepta orcadensis			x	x	x					
	Breutelia chrysocoma			x	x	x					
	Lophozia quinquedentata			x	x	x					
	Carex binervis	x	x	x	x	x					
	Hypericum pulchrum	x		x	x	x					
	Campylopus atrovirens			x	x	x					
	Erica cinerea	x	x	x	x	x					

TABLE 3 (*continued*)

Distribution type	Region no.	1	2	3	4	5	6	7	8	9	10
	Cladonia tenuis	x	x	x	x			x			
	Nowellia curvifolia			x							
	Lepidozia pearsonii				x						
	Hieracium schmidtii				x						
	– styctophyllum				x						
	Scapania compacta				x						
	– irrigua				x						
	Plagiochila denticulata				x						
	Mastigophora woodsii				x						
f.	Juniperus nana			x	x	x					
	Festuca vivipara			x	x	x					
g.	Gentianella campestris		x		x						
	Listera cordata			x	x	x					
	Lycopodium selago			x	x	x					
	Selaginella selaginoides			x	x	x					
	Ptilium crista castrensis				x	x					
	Sanguisorba officinalis		x			x					
	Rubus chamaemorus				x						
	Pyrola rotundifolia				x						
	– minor					x					
	Trollius europaeus				x						
	Dryopteris filix-mas				x						
	Sphagnum robustum				x						
	Dicranum bonjeani				x						
	Cladonia flabelliformis				x						
	– subcervicornis				x						
	Stereocaulon paschale				x						
	Linnaea borealis					x					
h.	Alchemilla alpina				x	x					
	Salix herbacea			x							
	Empetrum hermaphroditum				x						
	Saxifraga oppositifolia				x						
	Thalictrum alpinum				x						
	Dryas octopetala				x						
	Lycopodium alpinum				x						
	Juncus trifidus					x					

The overall percentage of atlantic species in this group is 57, that of the northern species 29; continental species are lacking. The difference with the preceding group with percentages for these elements of 25, 22, 24, respectively, is evident. The western heath is of a much more extreme nature than the northern heath. The percentages for the northern heath show it to be a meeting-ground of atlantic, boreal, and continental species. The percentages of widely distributed species in the northern and western heath are 29 and 14, respectively. This again reflects the extreme nature of the lastnamed vegetation.

2.4. *Species with preference for South-Atlantic heaths* Table 4

The optimal development of these species, as far as their occurrence in the heath is concerned, is in Southern Ireland, Cornwall, Brittany and outside of the region studied till the present, more to the South in the coastal regions of the Bay of Biscay. The low percentage of the widely distributed species (6 %) shows that this group, too, shows a strong preponderance of a certain element with a specialised character, in this case the mediterranean-atlantic element which comprises 65 % of the species. The species with an atlantic tendency in their distribution type make up together 93 %of the group. The total is 64, much less than in the preceding groups, where it is 96 and 86, respectively. Future studies in the heath South of Brittany will probably show this number to be much higher.

TABLE 4

Species with preference for south-atlantic heaths

Distribution type	Region no.	1	2	3	4	5	6	7	8	9	10
a.	Leontodon hispidus	x	x								
	Chrysanthemum leucanthemum	x	x								
	Stachys betonica	x	x								
	Ranunculus flammula		x	x							
b.	Radiola linoides	x									
	Hypericum humifusum	x									
	Sorbus torminalis	x									
	Serratula tinctoria	x	x								
	Carex flacca		x								
c.	Scilla verna	x	x								
	Cladonia imp. v. leucophaea	x		x							
	Corydalis claviculata	x									
	Hypericum helodes		x								
	Dryopteris borreri			x							
	– aemula			x							
	Saccogyna viticulosa			x							
	Adelanthus decipiens			x							
d.	Erica vagans	x	x								
	– ciliaris	x	x								
	– x watsoni	x	x								
	Agrostis setacea	x	x								
	Scilla autumnalis	x	x								
	Salix atrocinerea	x	x								
	Ulex minor	x	x								
	– europaeus	x	x								
	Anagallis tenella	x	x	x							
	Scutellaria minor	x	x	x							
	Parmelia trichotera	x		x							
	Lotus corniculatus ssp. maritimus	x									
	Daucus gummifer	x									
	Euphorbia portlandica	x									
	– paralias	x									

TABLE 4 (*continued*)

Distribution type	Region no.	1	2	3	4	5	6	7	8	9	10
	Senecio cineraria	x									
	Rubia peregrina	x									
	Asparagus off. ssp. prostratus	x									
	Dactylus glom. ssp. hispanica	x									
	Cirsium filipendulum	x									
	Symethis planifolia	x									
	Ruscus aculeatus	x									
	Lithospermum prostratum	x									
	Hypericum linarifolium	x									
	Helianthemum umbellatum	x									
	Tuberaria guttata	x									
	Astrocarpus purpurascens	x									
	Lobelia urens	x									
	Carum verticillatum	x									
	Sphagnum pylaiei	x									
	Asphodelus arrondeaui	x									
	– sphaerocarpus	x									
	Orobanche cruenta	x									
	Potentilla splendens	x									
	Erica scoparia	x									
	Cladonia endiviaefolia	x									
	Sedum anglicum	x									
	Pyrus cordata	x									
	Erica mediterranea			x							
	– mackai			x							
	Daboecia polifolia			x							
	Koeleria albescens			x							
e.	Cochlearia officinalis	x									
	Erica x praegeri			x							
	Saxifraga umbrosa			x							
	– spathularis			x							
j.	Allium schoenoprasum		x								

3. THE SPECTRA OF DISTRIBUTION TYPES

In the groups 1 through 10 in Table 5 all plant species have been compiled that were found in the heath of the regions under consideration. Ten different distribution types were distinguished. In most of the regions the widely distributed species form ca. 50 % of the total set of species; the subatlantic element is also rather evenly represented (13–19 %). The boreal-montane element, too, is always present, but shows much wider variation (4–17 %). To these three flora elements belong 227 species (= 59 %) of the total number of 384 recorded by the author in the North West European heath vegetations. This clearly demonstrates the affinity among the heath regions studied. The other flora elements are absent from one or more regions or have a representation of 1 % only. On the basis of the distribution of the last named flora elements, five regions may be distinguished.

TABLE 5

Spectra of distribution types of the heathland species recorded in 10 North-West European regions

Region no.	(%)										(number of species)									
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
widely distributed	37	52	41	41	47	57	54	49	51	63	70	65	64	90	70	47	83	76	94	64
subatlantic	17	18	16	13	13	18	16	19	13	14	32	23	25	29	20	15	25	30	24	14
atlantic	**11**	**9**	**14**	8	8	7	7	5	4	1	**20**	**11**	**21**	18	12	6	10	8	8	1
mediterranean atl.	**23**	**10**	5	3	—	—	—	—	—	—	**42**	**12**	8	6	—	—	—	—	—	—
eu-atlantic	**6**	2	**11**	**10**	**6**	1	1	1	—	—	**11**	3	**18**	**22**	**9**	1	1	1	—	—
boreal-atlantic	1	1	3	3	**7**	2	3	5	5	3	1	1	4	7	**10**	2	5	8	9	3
boreal-montane	4	7	9	**16**	**17**	**13**	**15**	**13**	**16**	8	7	9	14	**35**	**25**	**11**	**23**	**21**	**29**	8
arctic-alpine	—	—	1	**3**	1	—	—	—	—	—	—	—	1	**6**	2	—	—	—	—	—
central-meridional	2	1	1	1	1	—	1	3	**5**	3	4	1	1	3	2	—	1	4	**9**	3
continental	1	1	—	—	—	—	4	5	**7**	**9**	1	1	—	1	—	—	6	8	**13**	**9**
										Total	188	126	156	217	150	82	154	156	186	102

1. Brittany
2. Southern-England } South-atlantic
3. Ireland

4. Scotland and Wales } boreal-atlantic
5. Western-Norway
6. Southern-Netherlands and Belgium } subatlantic
7. Northern-Netherlands, N. Germany
8. Northern-Jutland } boreal-subatlantic
9. Southwest-Sweden
10. Southeast-Sweden boreal-subcontinental.

TABLE 6

Spectra of distribution types of the North-West European heathland species, according to their geographic preference devided in four separate groups

Group no.	(%)					(number of species)				
	1	2	3	4	5	1	2	3	4	5
a. widely distributed	6	14	29	**59**	32	4	12	28	**81**	125
b. subatlantic	8	8	9	**21**	13	5	7	9	**29**	50
c. atlantic	**13**	**13**	3	6	8	**8**	**11**	3	9	32
d. mediterranean-atlantic	**65**	7	—	—	13	**42**	6	—	—	48
e. eu-atlantic	6	**27**	—	—	7	4	**23**	—	—	27
f. boreal-atlantic	—	2	**13**	1	4	—	2	**12**	1	15
g. boreal-montane	—	**20**	**22**	10	14	—	**17**	**21**	14	52
h. arctic-alpine	—	**9**	—	—	2	—	**8**	—	—	8
i. central-meridional	—	—	**7**	3	3	—	—	**7**	4	11
j. continental	2	—	**17**	—	4	1	—	**16**	—	17
Total number						64	86	96	138	384

Group 1. Species with preference for south-atlantic heaths.
2. Species with preference for western heaths.
3. Species with preference for northern heaths.
4. Species widely distributed in the North-West European heath.
5. The total number of species (384) listed in the North-West European heath.

3.1. *The south-atlantic region*

Table 5a, no. 1, 2, 3. Brittany, Southern England, and Ireland.

Here the atlantic and the mediterranean-atlantic element have their optimum; the eu-atlantic element is also well represented. The flora elements with boreal or continental areas are much weaker represented than in other regions. The South Atlantic character is most pronounced in Brittany with 23 % of mediterranean-atlantic species. The overall percentage of species with atlantic affinities in Brittany is 58 % (106 species); consequently the percentage of widely distributed species (37 %) is much lower than elsewhere, but the absolute number of species of this type, 70, is not below the average.

3.2. *The boreal-atlantic region*

Table 5, no 4 and 5. Scotland, Wales and South-Western Norway.

The eu-atlantic element is well represented, as in the south-atlantic region, but there is much less of the less extreme western flora elements, viz. the atlantic and the subatlantic; this is naturally more true for the mediterranean-atlantic. The boreal ties are much stronger: the boreal-atlantic the boreal-montane, and the arctic-alpine flora element together comprise 22–25 % (in the preceding region 5–12 %). The presence of arctic-alpine species in this region has been noted already (§ 2.3).

3.3. *The sub-atlantic region*

Table 5, no 6 and 7. Belgium, Netherlands, North-Western Germany, Southern Jutland.

In this region the heath is notable by the absence of species reaching their optimum. This becomes evident when Tables 5 en 6 are compared. Group 1 (Table 6) has its optimum in the south-atlantic (Table 5, no 1, 2, 3), group 2 in the boreal-atlantic (Table 5, no 4, 5), group 3 in the boreal-subatlantic (Table 5, no 8, 9) and in the boreal-subcontinental region (Table 5, no 10). In Table 6 a group with its optimum in the subatlantic region could not be distinguished. Most constituents of the heath vegetation are widespread in this kind of vegetation in North-Western Europe. Only the 6 continental species in the northern part of the region are aberrant. The overall number of species is strikingly low in the southern part, 82, slightly more than half the number of the northern part. The difference is mainly due to the presence of continental species and of a larger number of species with a northern type of distribution on mineral rich soil, coastal and woodland species; but these are distributed among the flora elements in such a way that the constitution of both parts, relatively speaking, differs but little. The larger number of species with a northern type of distribution is not only due to the more northerly position but also to the Riss glaciation. The glaciers formed push moraines whose north-facing slopes provide favorable habitats for northern species (*Lycopodium clavatum*, *Polypodium vulgare*, *Trientalis europaea*, *Vaccinium vitis-idaea*, *Arctostaphylos uva-ursi*) and woodland species (*Dryopteris spinulosa*, *Anemone nemorosa*, *Hieracium laevigatum*, *Lonicera periclymenum*, *Hylocomium splendens*). The glaciers also deposited richer soils, boulder clay and consequently the heath contains more species than on the poor coversands to the South. Heathland species of the better northern soils are *Succisa pratensis*, *Campanula rotundifolia*, *Luzula multiflora*, *L. campestris*, *Antennaria dioica*, *Platanthera bifolia*. The presence, in the northern part, of coastal species (*Rosa pimpinellifolia*, *Carex trinervis*, *Carex arenaria*, *Genista tinctoria*) is due to the absence of lime in the sand of the coastal dunes North of Bergen on the Dutch coast. The coastal dune heath is well developed from Bergen to Cape Skagen but is absent from the dunes with a higher lime content to the South of Bergen and on the Belgian and northern French coasts. It does not reappear until Normandy, but here on the cliffs of acid rocks rather than in the dunes which are also rich in lime.

3.4. *The boreal-subatlantic region*

Table 5, no 8, 9. Northern Jutland, South-Western Sweden.

The phytogeographic spectra of this region show a characteristic combination of a rather high percentage (18 and 21 %, respectively) of boreal species with relatively rather many species with a continental or a central-southern European tendency (8 and 12 %, respectively). The percentage of atlantic species is lower than in the preceding regions.

3.5. *The boreal-subcontinental region*

Table 5, no 10. South-Eastern Sweden.

The continental tendency, low in the subatlantic region and slightly stronger in the boreal-montane region, is most noticeable in the North-West European heath in South-East Sweden (Damman, 1957) and in Eastern Denmark (Böcher, 1943), an offshoot of the subcontinental heath of Eastern Germany and Poland (Schubert, 1960). The total number of species (102) is the lowest in the regions studied, except in the Southern Netherlands and Belgium. This is partly due to the smaller size and consequently smaller variation. But the main reason is probably the climate. The annual precipitation in South-West Sweden is 600–1000 mm, in the heath areas of South-East Sweden only 500–600 mm (Damman, 1957). The formation of humus and leaching take place so intensively in the south western part that heath may occur even on originally neutral or even basic soils. Such heaths can be recognized by its herb-rich aspect with *Scorzonera humilis*, *Orchis maculata*, *Succisa pratensis*, *Solidago virgaurea*, *Lathyrus montanus*, *Sieglingia decumbens*, *Potentilla erecta*. In South East Sweden, however, such habitats are occupied by grassland of a continental type with *Anthericum ramosum*, *Helichrysum arenarium*, *Anthyllis vulneraria*, *Androsace septentrionalis*, *Satureja acinos*, *Artemisia campestris* and *Medicago falcata*. Here the heath covers the poor soils, also with continental species (9%): *Vicia cassubica*, *Viscaria vulgaris*, *Anemone pulsatilla*, *Artemisia campestris*, *Helichrysum arenarium*. The atlantic influence is the lowest of all areas studied (18%). The boreal influence (11%) is weaker than in the Southern Netherlands and Belgium and approaches that of Ireland and Southern England. An arithmetical consequence of this low percentage is the high amount of widely distributed species, 63%. The numerical relations between the flora elements and the low overall number of species show that the heath is here near the border of its distribution. The flora is quantitatively and qualitatively poorer than in the other regions; the only addition is the continental element, mostly consisting of grassland species. This shows a transition to the dry continental grassland vegetation. The same transition was described by SCHUBERT (1960) for Central Germany.

ACKNOWLEDGMENTS

The data used in this paper were collected during the following journeys: Netherlands, Belgium, North Western Germany (1959), Eire and Northern Ireland (1962), Brittany and Normandy (1963), Scotland, Wales and Southern England (1964), Southern Scandinavia and Northern Germany (1965). The main purpose of these journeys is the study of the European atlantic heath vegetations, to which a later paper will be dedicated.

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THE INDUMENT OF APEIBA AUBL. (TILIACEAE)

L. Y. TH. WESTRA

(*Botanical Museum and Herbarium, Utrecht*)

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Abstract

The indument on vegetative parts of Apeiba is examined. Some taxonomic problems left after Uittien's revision of the genus are reconsidered.

Introduction

The results presented here were obtained from a study of vegetative characters of the *Tiliaceae* of Suriname. This study was undertaken primarily to provide a key to sterile material of this family. In the course of the examination it was found that the *Apeiba* species possess some interesting features in their indument; at the same time it also became clear that publications by Uittien and Ducke on *Apeiba* had left some taxonomical questions without a satisfactory answer. This prompted me to investigate the trichomes with particular attention to the taxonomy. For practical reasons, however, I restricted myself to the indument on leaves and twigs. The (small) genus was taken in its entirety, thus including taxa outside Suriname as well.

Within *Apeiba* two sections can easily be distinguished: Sect. *Petoumo* Schum. and Sect. *Tibourbou* Schum. Within the first section four or perhaps five species are to be considered. *Apeiba echinata* Gaertn. appears to be very constant. The probably closely related *A. membranacea* Spruce ex Benth. is more variable, but usually it can be well distinguished from the first species. Some confusion has been caused by the presence of a few collections that more or less combine an *echinata*-like leaf indument with fruit characters of *A. membranacea*. One of these specimens seen by me belongs to a syntype collection of *A. macropetala* Ducke; Ducke himself reduced this species to a variety of *A. echinata* about thirteen years later. A. *intermedia* Uittien is known only from one tree in Suriname, several collections from which were made by the former Forestry Bureau. Uittien indicated its possible origin by hybridization between *A. echinata* and *A. glabra* (hence the name). *A. glabra* Aubl. is a well-marked species, very distinct from the others. Turning to Sect. *Tibourbou*, we find Ducke and Uittien against each other on the issue whether *A. albiflora* Ducke should be regarded as a species distinct from *A. tibourbou* Aubl. or not. It is true that the extreme forms are very different from each other and can easily be taken for two different species, but the picture is blurred by a number of collections appearing to be intermediate in one or several respects. *A. schomburgkii* Szyszyl. is easily distinguished from the other (two) species and seems to be less frequent, at least as far as I could judge from the smaller number of collections made. All other specific names referring to the genus *Apeiba* may be regarded as synonyms (see UITTIEN, 1935).

MATERIAL AND METHODS

Herbarium material largely from the Institute for Plant Taxonomy in Utrecht (Botanical Museum and Herbarium, U) and some from the New York Botanical Garden (NY) was examined. The tip of a dissecting needle was ground on one side and thus converted into a microchisel with which individual hairs could be excised under a dissecting microscope. These hairs could easily be gathered on a small clump of glycerin-gelatin put on the tip of another dissecting needle; this clump was then molten on a warm slide glass and served as the mounting medium. From objects with a very dense and appressed indument a small patch of the epidermis bearing a number of hairs was taken off in the same way; immersion in alcohol sometimes had to be applied prior to mounting in order to expel excess of air remaining among the hairs. Average figures are based on at least 20 measurements made at random on hairs on microscope slides. Not every herbarium specimen was examined this way, but a few samples were taken for each species (or variety), the number of samples depending upon the variability observed. All specimens were checked subsequently, however, by examining them *in toto* under a dissecting microscope, or a compound microscope in case they had very small hairs.

THE INDUMENT

Apeiba is characterized by the stellate hairs common to most representatives of the *Malvales*. These stellate hairs consist of a fascicle of unicellular hairs (called the rays) implanted in the epidermis. The rays are connected to each other at the basal part, where pits may be found too (Fig. 3, G), but are otherwise free. This is the type termed stellate hair ('Stern- oder Büschelhaare') by HUMMEL and STAESCHE (1962), see pp. 212–213, also fig. 7, B on p. 22 and fig. 79 on p. 196 (l.c.). In descriptive literature the term stellate hair is commonly used in a much wider sense, including a variety of hair types such as the unicellular star-shaped trichomes found in *Cruciferae* or various forms of uniseriate and pluriseriate hairs in several families. In some *Malvales* the rays are laterally connected to each other over a greater part of their length: this leads to the (stalkless) scales such as are found in the Tiliaceous genus *Mollia*. Within *Apeiba* a slight tendency towards this may sometimes be seen, especially in the leaf hairs of *A. glabra* (Fig. 2, B). The number of rays within a single stellate hair varies from two to numerous. In the *Tiliaceae* with stellate (or scaly) indument examined (besides *Apeiba*: species of *Luehea*, *Lueheopsis*, *Vasivaea*, *Triumfetta* and *Mollia*, *Heliocarpus popayanensis* H.B.K., *Christiania africana* DC.) the indument of the lower leaf sides appears to be more or less markedly different from that of petioles and twigs, the indument of large nerves usually being of a transitional type; the upper leaf sides usually have a thinner indument than the lower sides which reflects that of the latter or may be more or less transitional. In *Apeiba*, but this applies to the others mentioned as well, the rays of stellate hairs on the lower leaf sides are positioned at an angle with the epidermis varying from small (in more or less appressed stellae) to about 45–60 degrees, often being nearly equal for all rays within one stellate hair. The ray length usually does not vary much within one stella, and in most cases is not conspicuously variable within the same indument either, whereas the ray number often tends to stay fairly close to the average (usually 10 or less per stella). The whole impresses as a regular type of stellate indument when seen through a hand lens or microscope (Fig. 1, A, B, C, E; Fig. 2, A, B, E; Fig. 3, A, D, E, F; Fig. 4, A, B) [1]). The twigs and petioles are covered by a much more irregular type of indument, many of its constituent stellate hairs being tuft- or brush-like with rays oriented at angles with the epidermis varying from small to 90 degrees, often bent or curved in various ways, often variable in size within one stella, their number being equally variable, so that stellate hairs with 3 rays can often be found neighbouring ones with up to 30 (or even more) rays (Fig. 1, F, G; Fig. 2, C, D, G, H; Fig. 3, C, H, I, J; Fig. 4, D, E). It may be added briefly that inflorescence parts as peduncles, pedicels and outer side of sepals usually show the indument type of the twigs, but often in a more luxuriant form (greater density of stellate hairs, these on the average with more and larger rays). The stellate hairs on stipules and bract(let)s often tend towards a comparatively few-rayed type, with rays often irregular in appearance, esp. due to their way of curving or twisting.

The individual cells in all these hairs are usually fairly thick-walled; sometimes cell walls are so thick as to nearly obliterate the cell lumen except for in the basal part (Fig. 3, G).

Besides stellate hairs simple hairs can be found; this is a common feature not only of *Apeiba* but also of other Tiliaceous genera. Their shape is like that of the rays in stellate hairs, but they are often larger. In *Apeiba* Sect. *Petoumo* they are not very numerous, to be found chiefly on young and growing parts (twigs, petioles, large nerves) and fairly soon deciduous, thus often absent from older parts which may still be densely covered by stellate hairs. In Sect. *Tibourbou*, on the other hand, simple hairs are often abundant not only on young but also on adult parts.

In addition to stellate and simple hairs small glandular trichomes are present. HUMMEL and STAESCHE (1962), in their survey of plant hairs (l.c., p. 237), make mention of uniseriate glandular hairs in *Malvaceae*, *Tiliaceae* and *Bombacaceae*. It was observed by me that in *Tiliaceae* heads of glandular hairs often have vertical cell walls in addition to the horizontal walls (Fig. 1, H; Fig. 4, F). The head always appeared to be thicker than the stalk. The glandular hairs, as far as was seen, were outnumbered and often hidden by stellate hairs, thus making it practically very difficult to assess their taxonomical value. This survey, for that reason, will deal with stellate and simple hairs only.

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[1]) The comparatively large stellate hairs in Sect. *Tibourbou* are always somewhat squeezed between cover glass and slide glass and due to this these drawings, made with a microscope, do not exactly show the position of the rays as it would have appeared, could these hairs have been seen on the leaf surface in true three-dimensional view.

A SURVEY, WITH CRITICAL REMARKS

Some salient vegetative characters of *Apeiba* are: leaves usually elliptical to oblong-obovate, acute to acuminate, with 3 large primary nerves, the lateral ones usually not much longer than ½–⅔ of the length of the median one and similar in aspect to the secondary nerves of the median primary nerve (arcuate, coming close to the leaf margin and anastomosing with the first pair of secondary nerves), tertiary nerves parallel to each other and at right angles with secondary nerves, quaternary nerves repeating the pattern of the tertiary nerves, but tending towards becoming reticulate, the smallest veinlets reticulate; large nerves prominent below, flat or slightly prominent above; stipules oblong-lanceolate to lanceolate, early caducous in most species; indument of stellate hairs intermixed to a varying degree with simple hairs (esp. in Sect. *Tibourbou*).

Section **Petoumo** Schum.

Leaves entire to sometimes (faintly) dentate-serrate, hairs on lower side on nerves and in intervenulary areas, on upper side on nerves only. Conspicuous tufts of (brown) hairs often present at the base of the primary nerves on the lower side, sometimes also in the axils of the secondary nerves of the median primary nerve. Petioles more or less incrassate in their apical part.

Stellate hairs on vegetative parts with a ray length not exceeding 150 (–200) μ (with the exception of the tufted hairs at the base of large nerves). The majority of stellae on lower leaf sides appressed or moderately elevated (notably in *Apeiba echinata*), usually with moderately thick-walled rays having their largest width at or near the base (Fig. 1, A, B; Fig. 2, A, B, E; Fig. 3, A, D). Stellate hairs on large nerves, petioles and twigs more irregular in appearance, their rays curved and oriented in a more variable way and with their largest diameter at or near the base or somewhat higher; brown cell contents also noticeable in dried material (Fig. 1, F, G; Fig. 2, C, D, G, H; Fig. 3, C). Transitional hair forms to be seen on smaller nerves, especially on the upper side (Fig. 1, C, D, E; Fig. 2, F; Fig. 3, B). Stipules on their abaxial side, like bracts, with mostly few-rayed stellate hairs, the rays curved and twisted in a more or less irregular way. Simple hairs often fairly abundant on young, growing

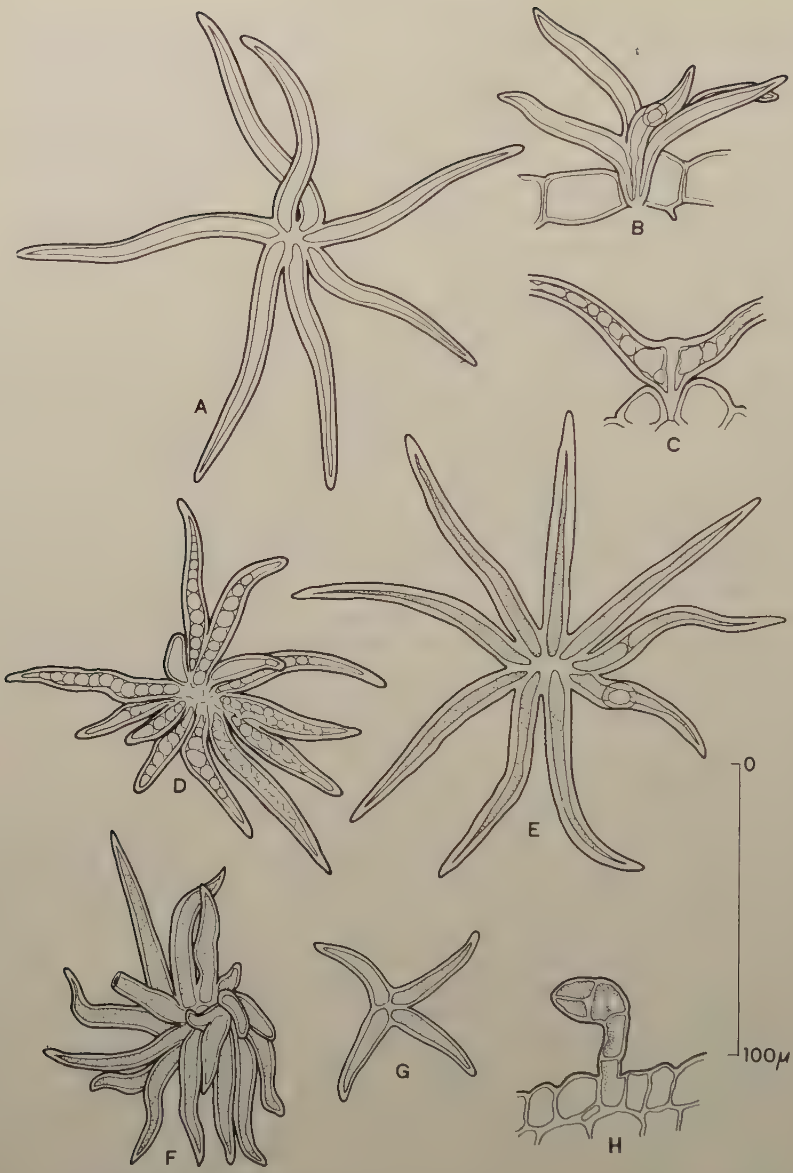

Fig. 1. **A. echinata.** A. Intervenular stellate hair from lower leaf side, top view. B. Same, lateral view, epidermis in sectional view. C. Venular stellate hair from lower leaf side, base in sectional view. D and E. Venular stellate hairs from lower leaf side, top view. F and G. Stellate hairs from petiole, top view. H. Glandular hair from median primary nerve, lower side, sectional view. (A through G from BW 4042; H from Lindeman 6464).

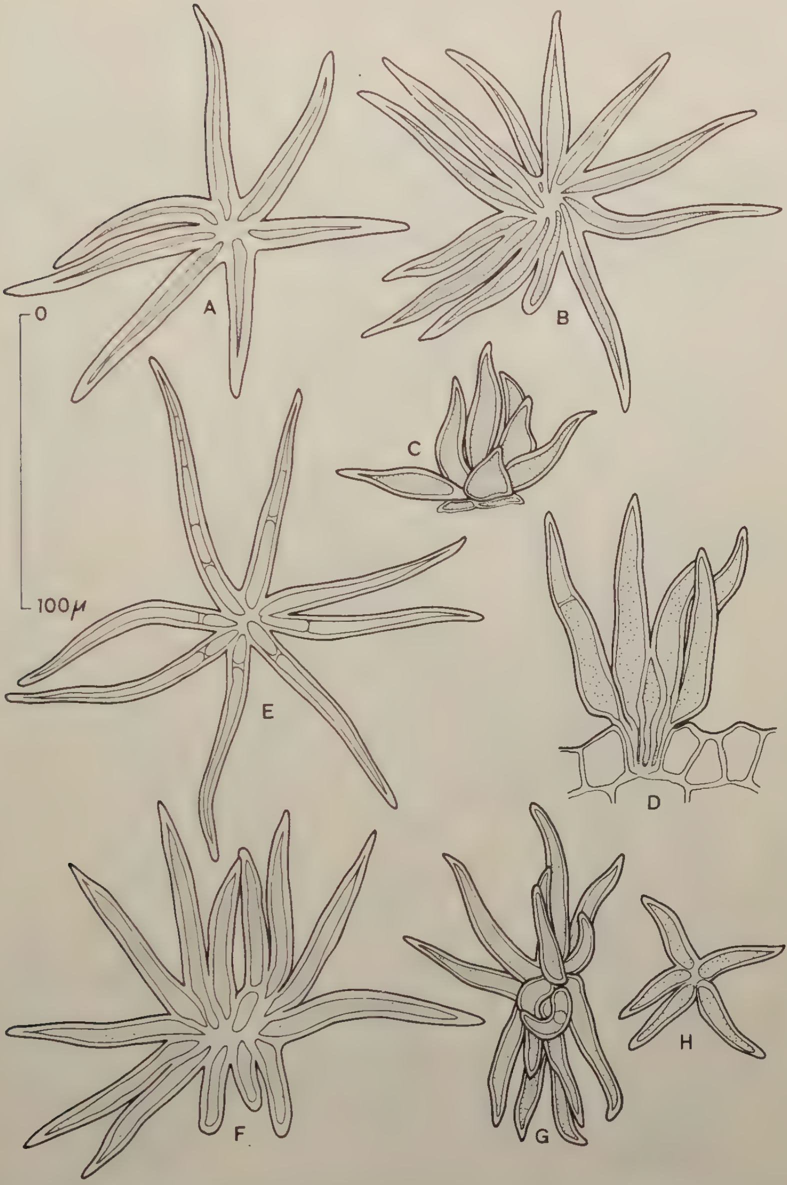

Fig. 2. **A. glabra.** A and B. Stellate hairs from lower leaf side, top view. C. Stellate hair from twig, lateral view. D. Stellate hair from petiole, sectional view. (from BW 6258).

A. intermedia. E. Intravenular stellate hair from lower leaf side, top view. F. Venular stellate hair from lower leaf side, top view. G and H. Stellate hairs from petiole, top view. (from BW 5592).

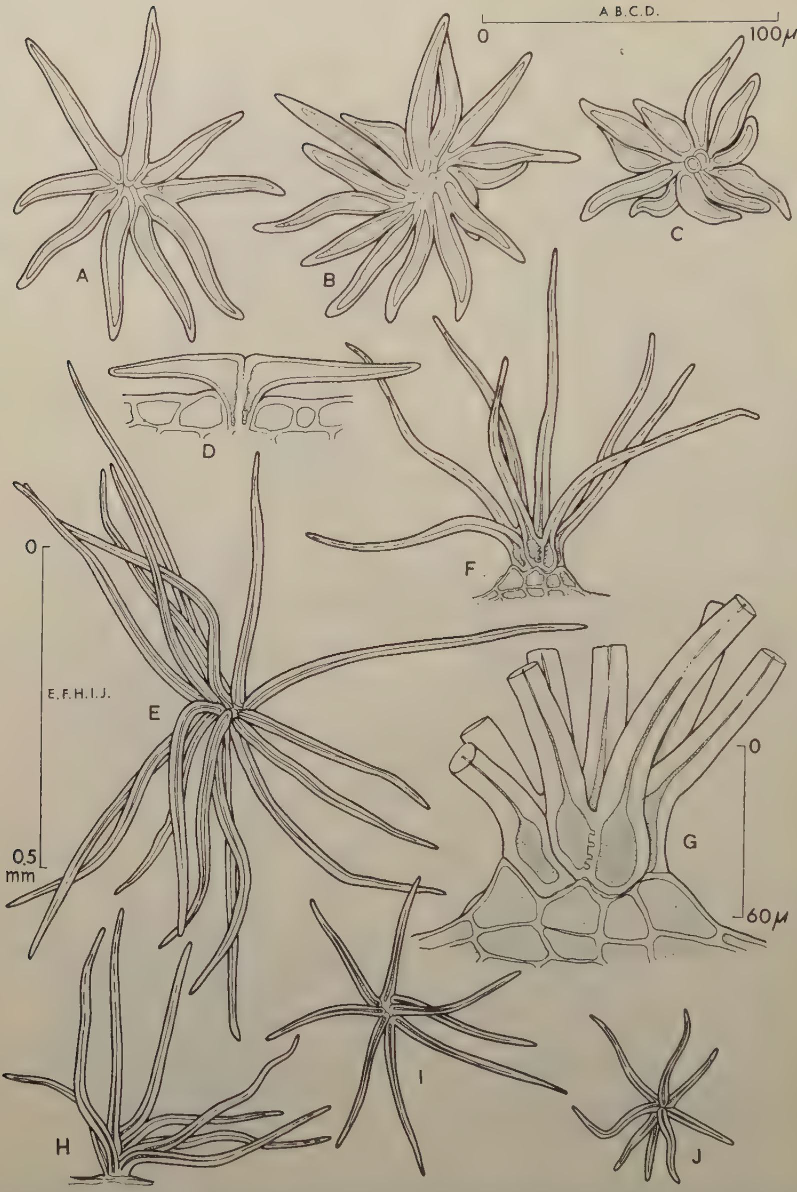

Fig. 3. **A. membranacea.** A. Intervenular stellate hair from lower leaf side, top view. B. Venular stellate hair from lower leaf side, top view. C. Stellate hair from petiole, top view. D. Intervenular stellate hair from lower leaf side, sectional view. (from Kuhlmann HJBR 18075).

A. schomburgkii. E. Stellate hair from lower leaf side, top view. F. Same, lateral view. G. Basal part of F, more enlarged. H. Stellate hair from median primary nerve, lower side, lateral view. I and J. Same, top view. (from Pulle 217).

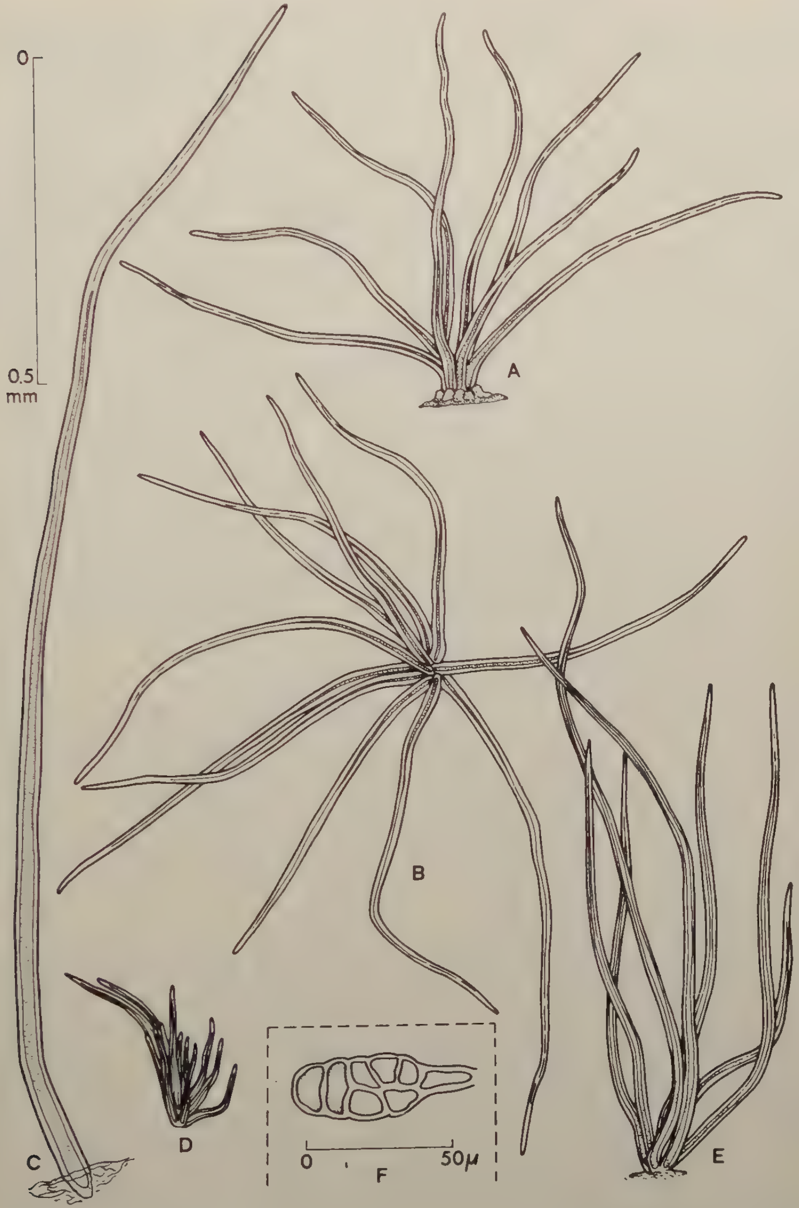

Fig. 4. **A. tibourbou.** A. Stellate hair from lower leaf side. lateral view, B. Same, top view. C. Simple hair from petiole. D and E. Stellate hairs from petiole, lateral view. F. Glandular hair from petiole head and part of stalk, lateral view. (A through E from Krukoff 1518; F from Krukoff 5291).

parts (large nerves, petioles, twigs), mostly appressed and not exceeding 1 mm in length, soon caducous and thus largely absent from older parts.

Apeiba echinata Gaertn.

Leaves 7–20 cm long and 4–10 cm wide, occasionally up to 30 cm long and 15 cm wide; first pair of lateral primary nerves ½–⅔ of the length of the median one, second pair weakly developped; secondary nerves (3–) 4–7 on each side of the median primary one. Upper leaf sides smooth, the nerves at most only slightly prominent; lower sides covered by a very dense mass of ± interwoven stellate hairs and nearly always with conspicuous tufts at the base of the primary nerves. Petioles (1–) 1½–2½ (–3) cm long, slightly incrassate apically over a length of about ½–1 cm.

Stellate hairs on lower leaf sides with 4–11 (–15), averaging ca. 8, rays of ca. 30–125 μ, averaging ca. 65–85 μ, long and with a largest diameter of 6–10 (–13) μ (Fig. 1, A, B); on small nerves stellae to be observed with a larger number of rays, that can be somewhat wider and sometimes are connate to each other to a little beyond the base (Fig. 1, C, D, E) – these hairs also present (scattered) on the upper side. The tufts consisting of stellate hairs more or less comparable to those on the petioles, but much larger in size, the rays (3–) 4–20, mostly directed upward, to 1–1½ mm long and 25 (–30) μ wide, often fairly thin-walled in comparison with the surrounding hairs. Large nerves, petioles and twigs (densely) covered by stellate hairs with (3–) 4–20 rays, these directed at often very variable angles, even within one stella (particularly in large hairs), about 20–80 μ, averaging ca. 40–50 μ, long and to 15 μ wide (Fig. 1, F, G). Simple hairs chiefly on very young parts, to ¾ mm long. Stellate hairs on stipules, abaxial side, mostly 4–8-rayed; simple hairs there to ½ mm long and 15 μ wide present or absent.

Two collections by Lindeman (nrs. 5428 and 6464, sterile material only) tend towards having a slightly thinner indument on the lower leaf sides than is normally found in this species, and the basal hair tufts are ± poorly developped in comparison with other collections. This may be due to the fact that those collections were made from young trees, indicated as 7 m and 3 m tall respectively. It should be added, however, that Lindeman 5956, while collected from a tree 4½ m tall, has leaves as observed from mature trees.

Material seen:

VENEZUELA, BOLÍVAR: Sierra Imataca, Rio Toro (Rio Grande) between Rio La Reforma and Puerto Rico, north of El Palmar, Steyermark 88124 (U).

BRITISH GUIANA: Matthews Ridge, Barima River, Northwest territory, Cowan 39373 (U); Essequibo River, Moraballi Creek, near Bartica, Sandwith 430 (U), 622 (U).

SURINAME: Coppename River, near Bitagron, Lindeman 6464 (U); Emma Range, Jonker and Daniels 1095 (U); Watramiri, tree nr. 1618, BW 1937 (U), 3454 (U), 3897 (U), 4042 (U), 4302 (U), 5003 (U), 5153 (U); Zanderij I, Wood Herbarium Surinam 205 (U); Sectie 0, tree nr. 702, BW 1386 (U), 3835 (U), 3949 (U), 4149 (U); Brownsberg, tree nr. 1031, BW 1774 (U), 6356 (U), 6749 (U), 6914 (U); ibid., tree nr. 1185, BW 3221 (U), 3435 (U), 4001 (U), 4702 (U); ibid., BW 3313 (U), 6512 (U); Osembo, Para River, BBS 89 (U); Peninica, BBS 1136 (U); Perica River, Commewijne Distr., Lindeman 5428 (U); Rikanau, near Moengo, Lindeman 5956 (U); Marowijne River, Armina Falls, BW 4177 (U); Tapanahony River, Manlobi, BW 3702 (U); without locality, Hostmann 294 (U, type coll. of *Apeiba hypoleuca* Steud.).

FRENCH GUIANA: Mana River, BAFOG 199M (U), 7007 (U); Cayenne, BAFOG 1052 (U), 1190 (U); Oiapoque River, Pedra Alice, 3° 40′ N, 52° 1′ W, Irwin, Pires and Westra 47559 (U).

BRAZIL, PARÁ: Upper Cupari River, plateau between the Xingú and Tapajós Rivers, Krukoff 1168 (U), 1186 (U).

Apeiba echinata, var. **macropetala** (Ducke) Ducke

No conspicuous hair tufts at the base of the primary nerves, but instead small tufts in the axils of the secondary nerves of the median primary nerve and also at the base of the primary nerves, or hair tufts totally lacking.

The indument often heavier than in the species (notably on upper sides of leaves and on petioles and twigs). Stellate hairs on lower leaf sides with rays of ca. 40–200 μ, averaging ca. 90–115 μ, long and 6–13 μ in largest diameter; on small nerves stellate hairs of even larger size, these with brown cell contents and thus easily visible among the surrounding mass when seen through a low-power microscope (25–50 ×). Tufts, if present, with rays up to 1 mm long and 20 (–25) μ wide. Large nerves, petioles and twigs also having a greater ray length than in the species, ca. 30–200 μ, averaging about 75–90 μ, with a largest diameter ca. 8–13 (–15) μ. Simple hairs on adult parts observable here and there among the stellate hairs, to ca. ½ mm long and 20 μ wide.

In his revision of the genus UITTIEN (1935) leaves some doubt as to how to separate *Apeiba echinata* from *A. membranacea*. His key distinguishes between leaves distinctly grayish tomentellous beneath with very conspicuous brown hair tufts at the base of the lateral primary nerves (called basal nerves) and depressed fruits ('concave top') for *A. echinata*, and leaves indistinctly tomentellous or nearly glabrous beneath with conspicuous brown hair tufts at the base of the lateral primary nerves and smaller tufts in the axils of the other (i.e. secondary) nerves, and fruits with a mammiform apex ('somewhat apiculate at the top') for *A. membranacea*. According to this, Ducke HJBR 24035 would match *A. membranacea* in its fruit shape and the small hair tufts at the base of the large nerves; its dense indument on the lower leaf sides, however, is distinctly 'echinata'-like. Uittien cites this collection under *A. membranacea*. Ducke HJBR 18080 is very similar: the fruit on the sheet in U is almost flat at the top, and as such it comes within the variability range of the *A. membranacea* fruit as observed by me, but it still is very different from the markedly depressed fruits on all the *A. echinata* material

I have seen; there are no hair tufts, but Uittien assumes that those have been eaten by insects, otherwise the dense indument on the lower leaf sides is again very 'echinata'-like. This collection, inconsequently, is cited by Uittien under *A. echinata* because of its leaf indument.

Apeiba macropetala Ducke (1925) was based, among others, on Ducke HJBR 18080; later on (1938) DUCKE reduced this species to a variety of *A. echinata* because he considered his collection Ducke HJBR 24035 as an intermediate. However, there is the fruit which is like that of *A. membranacea*, not at all like that of *A. echinata*, and this might indicate that Ducke's taxon should be placed at the specific rather than a lower level. Be it as it is, Ducke's solution apparently is a more consequent and natural one for the moment than that by Uittien, the indument providing an excellent character to distinguish readily between the taxa involved. Whether or not this will hold when more material will have been studied, remains yet to be answered.

Ducke, at first, thought that var. *macropetala* represented the species in the eastern half of the Amazon plain. Its area, however, appears not to be sharply separated from that of A. echinata, since it has been collected in British Guiana and since the species is now known from the Xingú and Tapajós Rivers region in Pará.

Material seen:

BRITISH GUIANA: basin of Essequibo River, near mouth of Onoro Creek at about 1° 35′ N, A. C. Smith 2775 (U).

BRAZIL, AMAZONAS: Rio Negro, Santa Izabel, Ducke HJBR 24035 (U); basin of Rio Solimões, municipality São Paulo de Olivença, basin of creek Belem, Krukoff 8289 (U); Parintins, Lago José-Assú, Ducke HJBR 34964 (U).

PARÁ: Belém, Ducke HJBR 18080 (U, syntype coll. of *A. macropetala* Ducke).

Apeiba glabra Aubl.

Leaves 9–15 cm long and 4–6 cm wide, first pair of lateral primary nerves $\frac{2}{3}$–$\frac{3}{4}$ of the length of the median one, second pair weakly developed (up to $\frac{1}{4}$ of the length of the first pair) to nearly obsolete; secondary nerves (2–) 3–4 on each side of the median primary nerve. Leaf surface often somewhat scabrid, the hairs barely visible to the naked eye, but appearing under a hand lens, varying from scattered to very numerous on the lower sides. No hair tufts at the base of large nerves, or only indicated by some stellate hairs of larger size. Petioles 1–2 cm long, somewhat thickened apically over $\frac{1}{2}$ to $\frac{3}{4}$ of their length.

Stellate hairs on lower leaf sides with about 4–20, averaging ca. 8–14, rays of ca. 30–115 μ, averaging ca. 55–80 μ, long and with a largest width of 9–12 μ, the rays often connate to each other somewhat beyond the base, thus making many hairs appear more or less scale-like (Fig. 2, A, B); largest stellate hairs with greatest ray number on small nerves; rays of stellate hairs at the base of large nerves sometimes to $\frac{1}{2}$ mm long and 20 μ wide. All leaf stellae containing brown cell substance, as hairs on other parts of the plant. Petioles and twigs with a dense cover of stellate hairs having 4–20 (–25) rays directed in very variable ways, particularly in large hairs, measuring ca. 25–110 μ, averaging ca. 40–55 μ, in length and 9–15 μ in largest diameter, sometimes up to 200 μ long and ca. 20 μ wide (Fig. 2, C, D). Simple hairs often quite numerous on younger parts, scattered or lacking on adult parts, up to ¾–1 mm long and 20–25 μ wide; occasionally stellate hairs observable one ray of which much exceeds the others in size and may become about equal to the simple hairs. Stipules with stellate hairs on abaxial surface with 3 to as many as 20 (–25) rays (as far as could be seen).

Material seen:

SURINAME: Wilhelmina Range, Julianatop, Schulz and Elburg LBB 10273 (U); Coppename River, near Bitagron, Lindeman 6465 (U); ibid., Raleigh Falls, Lanjouw 810 (U), BW 6153 (U), 6258 (U); Saramacca River, upper course, Pulle 231 (U); ibid., Jan Basi Gado, J. & P. A. Florschütz 1212 (U); ibid., Jacob Kondre, Maguire 23897 (U); ibid., Kwatta hede, Maguire 23913 (U); ibid., Paka Paka, Maguire 23969 (U); Upper Suriname River, Tresling 98 (U), 210 (U), 383 (U); Gonini River, BW 3707 (U).

FRENCH GUIANA: Beiman Creek, BAFOG 190M (U); Oiapoque River, Pedra Alice, 3° 40′ N, 50° 1′ W, Irwin, Pires & Westra 47555 (U).

BRAZIL, PARÁ: São Caetano de Odivellas, Ducke HJBR 15277 (U); Belém, Ducke HJBR 11267 (U), Pires 51747 (U); without locality, Burchell 9480 (U, syntype coll. of *Apeiba burchellii* Sprague).

Terr. AMAPÁ: Serra do Navio, Rio Amapari, Cowan 38082 (U).

Apeiba intermedia Uittien

Leaves 10–21 cm long and 5–8 (–9) cm wide, first pair of lateral primary nerves ½ (–⅔) of the length of the median one, second pair weakly developed; secondary nerves 5–6 (–7) on each side of the median primary nerve. Leaf surface smooth, the indument appearing under a low-power microscope, consisting of numerous, but still individually distinguishable, stellate hairs on the lower sides, scattered stellate hairs on the upper sides. Hair tufts present at the base of primary nerves and secondary nerves of the median primary nerve below, but not as conspicuous as those of *A. echinata*. Petioles about (1–) 1½–2 cm long, apically incrassate over a length of ca. ½–1 cm.

Stellate hairs on lower leaf sides with 4–10, averaging ca. 8, rays of ca. 30–100 μ, averaging ca. 80–85 μ, long and with a largest diameter of ca. 6–9 μ (Fig. 2, E); on small nerves and also on the upper sides stellate hairs with up to 15 (–20) rays to 13 (–15) μ in largest diameter and sometimes connate to somewhat beyond the base (Fig. 2, F). Stellate hairs from tufts with rays to ½–¾ mm long and 20 (–25) μ in largest diameter. Large nerves, petioles and twigs covered by stellate hairs with about 4–20 (–25) rays oriented at often very variable angles, particularly in larger stellate hairs, with a length of ca. 30–125 μ, averaging ca. 70–80 μ and with a largest diameter of 7–15 μ (Fig. 2, G, H). Simple hairs few, scattered, up to ¾ mm long and ca. 20 μ in largest diameter. Stipules on abaxial side with stellate hairs having an average of about 4 (to perhaps slightly more) rays up to ca. 110 μ long and 7–13 μ in largest diameter; also simple and geminate (or two-rayed stellate) hairs up to ½ mm long and 15 μ in largest diameter observable.

This species is known from Suriname only and all collections were made from the same, marked, tree. UITTIEN, when publishing it (1925), described it as an intermediate between *A. echinata* and *A. glabra* and thought it possibly might have originated by hybridization between those two species. Fruits were not available at that time. In 1931 twig fragments bearing mature fruits were collected, but they escaped Uittien's notice and thus the fruits remained unknown until recently, when they reappeared after a reorganization of the fruit herbarium in Utrecht. They are exactly like those of *A. echinata*. This does not give support to Uittien's speculation as to the hybrid origin of *A. intermedia*, for in that case a fruit more or less intermediate between that of *A. echinata* and that of *A. glabra* (which has more numerous and more slender spines) was likely to have been expected. *A. intermedia* is not conspecific with *A. membranacea* as suspected by MACBRIDE (1956), who, of course, could not know the fruits of *A. intermedia*. Fruit shape of *A. echinata* and *A. membranacea* is discussed under *A. echinata*, var. *macropetala*: everything said for *A. echinata* also applies to *A. intermedia*.

Apart from the fruits, *A. intermedia* resembles *A. membranacea*, but the foliar stellae (on the type material) of the first are somewhat larger and about equal those of *A. echinata* in size.

Material seen:

SURINAME: Brownsberg, tree nr. 1023 (type tree), BW 1727 (U), 5592 (U), 6370 (U), 6819 (U), s.n. (fruits) (U).

Apeiba membranacea Spruce ex Benth.

Leaves 7–21 cm long and 4–9 cm wide, first pair of lateral primary nerves about ½ of the length of the median one, second pair weakly developed; secondary nerves (4–) 5–7 on each side of the median primary nerve. Leaf surfaces smooth, the indument barely visible to the naked eye, but appearing at a magnification of 25–50 × and consisting of stellate hairs varying from scattered to (fairly) numerous on the lower sides, sometimes mainly concentrated along the larger nerves. Hair tufts at the base of primary nerves and secondary nerves of the median primary nerve, varying from quite conspicuous (but not as large as those of *A. echinata* to inconspicuous, sometimes almost absent. Petioles about 1–2½ cm long, with a slight apical thickening of about ½–1 cm.

Stellate hairs on lower leaf sides with 6–20, averaging ca. 8 (–10), rays of 15–85 (–110) μ, averaging ca. (40–) 50–60 μ, long and with a largest width of 6–12 μ (Fig. 3, A, D); largest stellae with greatest ray numbers, with rays sometimes connate to somewhat beyond the base, on small nerves (Fig. 3, B). Stellate hairs from tufts with rays to ½–1 mm long and 20 (–25) μ in largest diameter. Large nerves, petioles and twigs densely covered by stellate hairs to nearly glabrous, these stellate hairs with about 4–20 rays ca. 25–140 μ long, averaging ca. 55–80 μ, and ca. 7–12 (–15) μ in largest diameter, directed at often very variable angles, especially in larger hairs (Fig. 3, C). Some simple hairs occurring among the stellate hairs, to $\frac{1}{2}$–$\frac{3}{4}$ mm long (occasionally up to 1$\frac{1}{2}$ mm) and 20–25 (–30) μ wide. Stipules on abaxial side with stellate hairs with 2–10, averaging ca. 5–6, rays with an average length of ca. 80–85 μ and a largest diameter of 7–12 μ; also with some simple and geminate (or two-rayed stellate) hairs to ca. 350 μ long and 15 μ wide.

See remarks under *A. echinata*, var. *macropetala*, and *A. intermedia.*

Material seen:

PANAMA, DARIEN: Rio Chico, vicinity of Yaviza, P. H. Allen 4578 (U).

COLOMBIA, AMAZONAS: Rio Putumayo, near mouth of Rio Igaraparaná, Schultes 3987 (U).

VENEZUELA, AMAZONAS: Casiquiare, Vasiva, and Pacimoni Rivers, Spruce 3204 (NY, syntype coll.).

BRITISH GUIANA: Bartica-Potaro Road, Forest Dept. F1465-4201 (NY).

BRAZIL, AMAZONAS: basin of Rio Solimões, municipality São Paulo de Olivença, near Palmares, Krukoff 8101 (U), 8170 (U); basin of Rio Juruá, near mouth of Rio Embira (tributary of Rio Tarauacá), 7° 30′ S, 70° 15′ W, Krukoff 5016 (U); basin of Rio Madeira, municipality Humaitá, near Três Casas, Krukoff 6186 (U); ibid., near Livramento, on Rio Livramento, Krukoff 6580 (U).

Terr. ACRE: basin of Rio Purus, near mouth of Rio Macauã (tributary of Rio Iaco), 9° 20′ S, 69° W, Krukoff 5304 (U); between Rio Abunan and Rio Acre, Kuhlmann HJBR 18075 (U).

BOLIVIA, LA PAZ: Larecaja, Tuiri (near Mapiri, on left bank of Rio Mapiri), Krukoff 10736 (U); ibid., Mapiri, Rusby 723 (NY).

Section **Tibourbou** Schum.

Leaves (crenate-) serrate, with hairs on nerves only (the number of hairs per nerve roughly proportional to nerve size on the lower sides, hairs on upper sides more evenly distributed on nerves). No hair tufts at base of nerves. Petioles not or but slightly incrassate in their apical part.

Stellate hairs on vegetative parts with rays up to $\frac{1}{2}$–1 (–2) mm long, with brown cell contents (in sicco). Those on small nerves with rays mostly directed upward at a fairly large angle, thick- to very thick-walled, the largest width usually at the base, the entire stella sometimes on a slight elevation (Fig. 3, E, F, G; Fig. 4, A, B). Stellate hairs on primary nerves, petioles and twigs with somewhat more irregularly bent or directed rays (Fig. 3, H, I, J; Fig. 4, D, E), the stellate hairs on secondary and tertiary nerves being ± transitional. Simple hairs on large nerves, petioles and twigs often conspicuous, the petioles and twigs then hirsute by spreading hairs to 2–3 mm long (Fig. 4, C), the nerves with more appressed hairs, at least on the lower sides; simple hairs on secondary and smaller nerves of smaller size, to about as long as the rays. Stipules and bracts on the abaxial side with mostly appressed simple hairs (shorter than those on the twigs), all or most of them confined to the middle zone, the margin ciliate by simple hairs of somewhat smaller size; comparatively small and few-rayed stellate hairs also present.

Apeiba schomburgkii Szyszyl.

Leaves 12–23 (–24) cm long and 6–11 cm wide, first pair of lateral primary nerves ⅓–½ of the length of the median one, second pair weakly developed; secondary nerves (5–) 6–7) (–8) on each side of the median primary nerve. Large nerves somewhat prominent above, quite prominent below. Both leaf sides stellate hirsutulous-pubescent, the lower more densely so. Petioles 1–2 cm long, very slightly incrassate (over a length of ½–1 cm) or not incrassate at the apical end.

Stellate hairs on tertiary and smaller nerves on lower sides often on small elevations, with (2–) 4–20 (–25), averaging about 8–12, rays of 0.15–0.80 (–1.00) mm, averaging ca. 0.50–0.60 mm, long and with a largest width of ca. 15–22 μ, with brown-yellow cell walls, the cell lumen nearly obliterated except at the base (Fig. 3, E, F, G). Stellate hairs on upper leaf sides somewhat differing from those below: rays 2–10, averaging about 4–6, ca. 0.10–0.40 mm, averaging ca. 0.20–0.30 mm, long. A few simple hairs similar in size and shape to the rays occurring among the stellate hairs. Large nerves, petioles and twigs with an indument varying from fairly dense to rather sparse: stellate hairs with more variably directed rays than those on the leaves, also somewhat smaller, ca. 0.07–0.70 (–1.00) mm, averaging ca. 0.25–0.40 mm, long (Fig. 3, H, I, J); numerous simple hairs among the stellate hairs, often exceeding them in number and mostly on distinct elevations, to 2½–3 mm long and ca. 40 μ in largest diameter. Stipules on their abaxial side with simple hairs to 2 mm long and with similar hairs to 1½ mm long on the margin; stellate hairs with an average of about 4–5 rays, these (30–) 50–200 (–250) μ long and with a largest diameter of ca. 10–13 μ, mostly appressed or slightly elevated.

Material seen:

TOBAGO: Bacolet, Sandwith 1874 (U); valley of Doctor's River, SE of Charlotteville, Webster, Ellis and Miller 9822 (U).

TRINIDAD: Cascade, Beard 138 (U); Botanic Garden, Kostermans A15043 (U).

BRITISH GUIANA: Western extremity of Kanuku Mts., in drainage of Takutu River, A. C. Smith 3111 (U).

SURINAME: Corantijn River, Tramway Falls, Rombouts 155 (U); Voltzberg, Pulle 217 (U, type of *Apeiba surinamensis* Uittien).

BRAZIL, AMAZONAS: Upper Rio Branco, Bôa Vista, Kuhlmann HJBR 3513 (U).

Apeiba tibourbou Aubl. (including **A. albiflora** Ducke)

Leaves 14–35 (–40) cm long and 6–15 (–17) cm wide, first pair of lateral primary nerves ⅓–½ of the length of the median one, second pair varying from weakly developed to manifest, up to ca. ⅓ of the length of the first pair, a third pair often discernible. Secondary nerves 8–12 (–13) on each side of the median primary nerve. Lamina slightly rugose (almost flat only in Wurdack and Guppy 113) to very rugose, stellate-pubescent to hirsutulous on both sides. Petioles 1–3½ cm long, not incrassate or (in comparatively long-petioled specimens) faintly incrassate at the apical side over a length of ½–1½ cm. Stipules often fairly persistent, remaining much longer than in other *Apeiba* species, 1½–3 cm long, 4–8 mm wide.

Stellate hairs on lower leaf sides on small elevations or not, with 4–15 (–20), averaging about (6–) 8–10, rays 0.2–1.0 (–1.2) mm, averaging ca. 0.6–0.7 (–0.8) mm, long and with a largest diameter of 12–17 μ, with colorless to faintly brown-yellow cell walls, the cell lumen widest at the base, narrow elsewhere; densest indument, along with greatest ray numbers, observed on tertiary nerves, greatest ray lengths (often) on quaternary nerves (Fig. 4, A, B). Stellate hairs on upper leaf sides with ca. 2–10, averaging ca. 4–5, rays of ca. 0.2–0.8 (–1.0) mm, averaging ca. 0.3–0.5 mm, long and with a largest diameter up to 20 μ, the stellae with most rays again on tertiary nerves; specimens with very rugose leaves bearing very few hairs on quaternary and smaller nerves on upper side. Simple hairs on upper leaf sides mostly of same size as rays, sometimes up to 1½–2 mm long and 25 μ in largest diameter. Indument of primary and secondary nerves more or less transitional.

Indument of petioles and twigs showing two extremes, in combination with certain other characters, viz.:

I. Petioles and twigs densely villous with predominantly stellate hairs having less than 8 (–10) rays on the average, these rays to 2 mm long, averaging ca. ¾–1 mm, and usually directed upward at an angle close to 90 degrees (compare Fig. 4, E). Simple hairs on twigs not exceeding stellate hairs in length and also (far) less in number than those, on petioles (and large nerves) sometimes more evident. Leaves strongly rugose, commonly oblong and mostly shorter than 20 cm; petioles ca. 1–1½ cm long, not incrassate.

II. Petioles and twigs hirsute with a great number of spreading simple hairs up to 3 mm long and 30–40 (–50) μ in largest diameter (Fig. 4, C), furthermore covered in somewhat variable degree by stellate hairs with rays up to 2 mm long (fig. 4, E), but averaging not more than about ½ mm (often much less), the average ray number usually 10 or more per stella (largest numbers in small ones), the rays directed at very variable angles even within one stellate hair (Fig. 4, D). Leaves mostly somewhat rugose, elliptic to elliptic-oblong, mostly longer than 20 cm; petioles ca. 2–3½ cm long, slightly incrassate apically or not.

Stellate rays in both groups from ca. 50 μ to ca. 2 mm long and with a largest diameter of ca. 10–20 (–25) μ. Stipules on abaxial side with simple hairs to 2–2½ mm long, the margin with (often comparatively thin-walled) simple hairs up to 1 mm long; stellate hairs more or less covering the entire abaxial surface or largely confined to the middle zone, with 2–10, averaging ca. (5–) 6 (–7), rays to 0.2 mm long and ca. 12 μ in largest diameter.

Most of the specimens examined can be placed in one of the two groups just described, hence to be referred to as group I and group II respectively. The material collected in the Guiana's largely comes within group I. The typical collections may be enumerated:

I. Breteler 3867, Fanshawe in Forest Dept. 3438, Fanshawe s.n., Fanshawe in Forest Dept. 3354, Schulz and Elburg LBB 10124, Lindeman 4750, Schulz 8513, Exp. Wilhelmina Geb. 71, BAFOG 7280, Sagot s.n., Black 47–1901, Lisbôa HJBR 4730.

II. Holm and Iltis 247, Dodge *et al.* 16631, Johnston 8, Harris 6506, Schulz 35, Vogl 702, Wurdack and Guppy 113, Krukoff 5291, 1074, Huber Herb. Mus. Goeldi 9333, Fróes 1807, Krukoff 1518, Klug 4213.

Group I conforms to *Apeiba albiflora* Ducke (1922); Lisbôa HJBR 4730 is one of the collections on which Ducke based his species; see also remarks by Burret apud Ducke (1938), p. 51. Group II, then, is *A. tibourbou* in the proper sense. White flowers and more globular fruits with very long and softer spines are mentioned as characters to distinguish *A. albiflora* from *A. tibourbou*. Uittien, in his revision of the genus (1935), concludes that the fruit shape is variable and cannot be relied upon and states that the white flower color is of no importance at all for the taxonomy of a genus which includes species with white flowers (*A. schomburgkii*) and yellow flowers as well. One may object to this statement, taken in its absolute sense, but in *Apeiba tibourbou/albiflora* collector's data on flower color are too scarce and sometimes vague and cannot have much conclusive force yet. Uittien, for those reasons, puts *A. albiflora* under synonymy with *A. tibourbou*.

As to vegetative characters examined by me, specimens intermediate in one or more respects were found. These will be commented upon now. Steinbach 6707 has very rugose, elliptic leaves with petioles to 2 cm long and slightly incrassate apically, the indument being conform to that of group I (petals indicated as white); Lanjouw 935 agrees in its leaf shape and size with group I, but the lamina is less rugose than in the collections cited above, the indument, with simple hairs clearly in evidence, tending towards that of group II; Dumortier 18 conforms to group I except for its elliptical leaves; also largely belonging to group I are Maas and Tawjoeran LBB 10902 and Lindeman 6197, the indument in the first somewhat tending towards that of group II, as also does to some extent that in the second, the leaves of which, in addition being less rugose than average in group I. On the other side there are two collections belonging to group II in most respects, but one, BAFOG 7840, has petioles only $1\frac{1}{4}$–$1\frac{1}{2}$ cm long and a lamina more rugose than is normally seen in group II, and the other, Breteler 3910, has an indument tending towards that of group I. A short glance I could take at the herbarium material in NY (not cited, because lack of time kept me from a more extensive microscopical examination) made me suspect that several other collections could augment this series.

It seems wisest, in view of this, to stick to Uittien's decision now and regard the whole *A. tibourbou* complex as a single, variable, species. Ducke's concept certainly has some appeal, and eventually may still prove to be right, but extensive investigation of more material must be carried out first.

Material seen:

Costa Rica, Puntarenas: vicinity of Cascajal, 25 km ESE of Puntarenas, Holm and Iltis 247 (U).

Panama, Panama: along road between Panamá and Chepo, Dodge *et al.* 16631 (U).

Perlas Archipelago: San José Island, Johnston 8 (U).

Jamaica: Hope, Harris 6506 (NY).

Venezuela, Barinas: Pedraza, Ticoporo, Rio Bumbum, Schulz 35 (U); Ticoporo Forest Reserve, bank of Rio Bumbum, 8° 15′ N, 70° 45′ W, Breteler 3910 (U).

Sucre: Las Penas, Vogl 702 (U).

Bolívar: Hato de la Vergarena, Rio Saca, Wurdack and Guppy 113 (NY).

Near the border (= Rio Grande o Toro) between Edo. Bolívar and Terr. Delta Amacuro, ca. 8° 4′ N, 61° 44′ W, Breteler 3867 (U).

British Guiana: Mazaruni Station, Fanshawe in Forest Dept. 3438 (U), Fanshawe s.n. (NY); Essequibo River, Tiger Creek, Fanshawe in Forest Dept. 3354 (NY).

Suriname: between Lucie River and Wilhelmina Range, Schulz and Elburg LBB 10124 (U); Nickerie River, near Blanche Marie Falls, Maas and Tawjoeran LBB 10902 (U); Voltzberg, Lanjouw 935 (U); Suriname River, Jodensavanne, Mapane Creek area, Lindeman 4750 (U), Schulz 8513 (U); ibid., upper course, near Goddo, Exp. Wilhelmina Geb. 71 (U); between Moengo Tapoe and Coermotibo Creek, Lindeman 6197 (U); without locality, Dumortier 18 (U).

French Guiana: St. Laurent, BAFOG 7280 (U); Tampoc River, BAFOG 7840 (U); Acarouany, Sagot s.n. (U).

Brazil, Terr. Acre: near mouth of Rio Macauã (tributary of Rio Iaco), 9° 20′ S, 69° W, Krukoff 5291 (U).

Pará: Belterra, Black 47–1901 (U); Upper Cupari River, plateau between Xingú and Tapajós Rivers, Krukoff 1074 (U); Belém, Huber Herb. Mus. Goeldi 9333 (U).

Maranhão: Maracassumé River region, Fróes 1807 (U); Cururupú, Lisbôa HJBR 4730 (U, syntype coll. of *Apeiba albiflora* Ducke).

Matto Grosso: near Tabajara, Upper Machado River region, Krukoff 1518 (U).

Peru, San Martín: Juan Jui, Alto Rio Huallaga, Klug 4213 (U).

Bolivia, Santa Cruz: Sara, Buena Vista, Steinbach 6707 (U).

Apeiba tibourbou, var. **krukoffii** Uittien

Leaves 20–30 cm long, 6–9 cm wide, with 5–7 (–8) secondary nerves on each side of the median primary nerve; lamina oblong to oblong-obovate, very rugose and thin. Petioles 1–1½ cm long, not incrassate. Stipules as with the species, 1–1½ (–2) cm long and 2–3 (–4) mm wide.

Leaves more sparsely hairy (except for large nerves) than in the species; stellate hairs on lower leaf sides with 2–8, averaging ca. 5, rays up to 1¼ mm long, averaging ca. 0.7–0.8 mm, on upper leaf sides with 2–6, averaging ca. 3 (–4), rays often directed upward at a large angle, up to 1½ mm long, averaging ca. ¾–1 mm, with a largest diameter to ca. 20 μ; a few simple hairs among the stellae, equal in size and shape to the rays. Large nerves, petioles and twigs with a dense indument (that of the twigs sligthly thinner than that of the petioles, otherwise similar); stellate hairs as described for group I under A. tibourbou, but simple hairs present as in group II, to 3–3½ mm long and 40–50 μ wide.

The above description applies to the type specimen which was the only one known to Uittien. Uittien's citation of Harris 6506 from Jamaica must be a mistake: the material seen by me in NY agrees with *A. tibourbou*, group II, and BURRET (in DUCKE, 1938) rightly calls it 'a typical tibourbou'. More recently, Lindeman collected sterile twigs in Surinam (Lindeman 6149) with leaves conspicuously resembling those of var. *krukoffii*; they are slightly smaller and somewhat less rugose. The indument on the lower leaf sides is similar to that of the type, but the hairs are somewhat smaller on the average; on the upper leaf sides simple hairs are slightly more numerous than in the type. The indument of petioles and twigs, however, is that of group II.

BURRET (l.c.) reckons the type collection of var. *krukoffii* to *A. albiflora*. Although it indeed seems to come closest to group I (or *A. albiflora*), it is certainly not perfectly identical with that, as Burret would have it. Scarcity of material does not warrant any conclusions as to the status of var. *krukoffii* at this moment.

Material seen:

SURINAME: between Moengo Tapoe and Coermotibo Creek, Lindeman 6149 (U) (provisionally placed here).

BRAZIL, MATTO GROSSO: source of the Jatuarana River, Machado River region, Krukoff 1567 (U, type).

KEY TO THE SPECIES OF APEIBA, BASED ON VEGETATIVE CHARACTERS

The foregoing may be summarized in the following key:

1. Leaves entire or (faintly) serrate-dentate near the apex, with stellate hairs with rays not or rarely more than 150 μ long, the stellae thus barely discernible by the naked eye, with the exception of hair tufts often present at the base of large nerves; simple hairs on petioles and twigs few, inconspicuous, or lacking (Sect. **Petoumo**) 2

   Leaves (crenate-)serrate, with stellate hairs with rays to ½–1½ mm long, the stellae thus easily discernible by the naked eye; no hair tufts at the base of nerves; simple hairs often many, conspicuous (Sect. **Tibourbou**) . . 6

2. First pair of lateral pirmary nerves ⅔ or more of the length of the median one, the latter with 3–4 secondary nerves on each side; stellate hairs on leaves often somewhat scale-like . . . . **A. glabra**

   First pair of lateral primary nerves about ½ (to ⅔ at the most) of the length of the median one, the latter usually with 5 or more secondary nerves on each side; stellate hairs on leaves (some venular stellae excepted) not scale-like 3

3. Lower leaf sides covered by a dense tomentum of stellate hairs so close together as to be undistinguishable individually (a few venular stellae excepted) 4

   Stellate hairs on lower leaf sides distinguishable individually or the majority of them so; hair tufts at the base of large nerves on lower sides present, sometimes inconspicuous 5

4. Nearly always conspicuous hair tufts at the base of lateral primary nerves on lower sides, no tufts elsewhere; average ray length of stellate hairs on lower leaf sides (usually) less than 90 μ . . . . **A. echinata**
   (Very) inconspicuous hair tufts at the base of secondary nerves of the median primary nerve on lower side present or absent; average ray length of stellate hairs on lower leaf sides more than 90 μ . . . . **A. echinata,** var. **macropetala**
5. Stellate hairs on lower leaf sides with an average ray length more than 70 μ . . . . **A. intermedia**
   Stellate hairs on lower leaf sides with an average ray length less than 70 μ . . . . **A. membranacea**
6. Leaves without raised mesophyll, stellate hairs on small nerves below with rays 15–22 μ in largest diameter, with brown-yellow cell walls . . . . **A. schomburgkii**
   Leaves slightly to strongly rugose; stellate hairs on small nerves below with rays 12–17 μ in largest diameter, with colorless to, at most, faintly brown-yellow cell walls 7
7. Leaves slightly to strongly rugose with an obvious to quite dense stellate indument, stellate hairs on small nerves below with up to 15(–20), averaging mostly 8–10, rays . . . . **A. tibourbou** (**s.l.**: 8)
   Leaves strongly rugose, quite glabrous in appearance, with scattered stellate hairs, rays on small nerves below to 8 per stella, averaging ca. 5 . . . . **A. tibourbou,** var. **krukoffii**
8. Leaves strongly rugose, mostly shorter than 20 cm; simple hairs, at least on twigs, not exceeding stellate hairs in length. . . . . **A. albiflora**
   Leaves slightly rugose, mostly longer than 20 cm; simple hairs on twigs conspicuously exceeding stellate hairs in length . . . . **A. tibourbou s.s.**)

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SOME OBSERVATIONS ON THE TRANSITION ZONE BETWEEN THE XEROSERE AND THE HALOSERE ON THE BOSCHPLAAT (TERSCHELLING, THE NETHERLANDS) WITH SPECIAL ATTENTION TO CENTAURIUM VULGARE RAFN

A. H. J. FREIJSEN

(*Biological Station 'Weevers' Duin', Oostvoorne, the Netherlands*)

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ABSTRACT

Three important plant communities were studied on the salt marsh "the Boschplaat" on the Westfriesian island of Terschelling: the *Centaurieto-Saginetum moniliformis* D., S. et W. 1940, the *Sagineto maritimae-Cochlearietum danicae* Tx. et G. 1957 and the *Juncetum gerardii* W. 1906 (Table 1). The boundary lines of these associations are determined by soil moisture, salinity and density of vegetation.

Five bare field plots were prepared in the transition zone. The establishment of species was followed during one year. For most species the original pattern was rapidly restored with some exceptions e.g. *Centaurium vulgare* Rafn (Table 3). Life-cycle and distribution pattern of *Centaurium vulgare* were more exactly investigated on one field plot (Table 4). Competition, density of adult plants, density of seedlings and soil moisture appeared to de dependent on each other in this sequence.

1. THE LOCALITY

The underlying survey was performed on the salt marsh 'the Boschplaat', which forms the eastern point of the Westfriesian island of Terschelling. This salt marsh is periodically inundated from the south. On the northern side of the Boschplaat a sand dike stretches from west to east. On the south coast there occur four dune-groups: Eerste, Tweede, Derde and Vierde Duintjes ('First, Second, Third and Fourth Little Dunes'). These four dune-groups are separated by tidal channels. Through these channels the water of the Wadden-Sea inundates the salt marsh. The 'Duintjes' are only partly inundated by storm-floods.

Between sand dike and dune-groups there occur numerous very small dunes on the salt marsh. These almost round dunes possess as a peculiar feature an almost bare sandy zone shaped like a horseshoe. The upper boundary of the bare zone is formed by the storm-flood mark in a *Koelerion*-community, its lower boundary is formed by the upper limit of the highest community of the halosere: the *Juncetum gerardii*. The convex side of the horseshoe is exposed to the west. The horseshoes originate from the erosion by storm-floods from western directions.

The investigations on the Boschplaat – comprised in this paper – were performed on some of the "horseshoe" dunes unless stated otherwise. For further information about the locality of this survey the reader may be referred to: De Fouw (1963), Visser (1947), Westhoff (1947 and 1951).

2. The vegetation

Table 1 renders a brief survey of the plant communities between the levels of storm-flood and spring tide on the Boschplaat. It is composed of fifteen sample plot analyses made according to the method of Braun-Blanquet (1951, 1932) in the summers of 1962 and 1963. The first five columns give an impression of the association: *Centaurieto-Saginetum moniliformis* Diemont, Sissingh et Westhoff, 1940. This plant community occurs just above the boundary line between the xerosere and the halosere: 154 cm + N.A.P. ('New Amsterdam Level') [1]). On the horseshoe dunes vegetations of this type are found in the rather open horseshoe zone. This community consists of three groups of species. First there is a group of true dune plants mainly belonging to the alliance: *Koelerion albescentis* (Braun-Blanquet 1936) Weevers 1940. One of these dune plants is *Festuca rubra* ssp. *rubra* var. *arenaria* Fries, which is often the dominant species. The second group is composed of halophytes. These species often possess a reduced vitality on this level of the salt marsh, but they demonstrate the still existing influence of the salt factor.

Centaurium vulgare Rafn[2]) and *Sagina nodosa* var. *moniliformis* Meyer – in the middle group of species in Table 1 – are the faithful species of the *Centaurio-Saginetum*. Both species possess an optimal development in this zone on the Boschplaat. As pioneer plants they prefer an open, sandy and moist soil. *Centaurium vulgare* is oligohalobious according to Freijsen (1964). *Sagina nodosa* is salt-tolerant. The *Centaurio-Saginetum* is also met with in young primary dune valleys which are just being cut off from the sea. Most descriptions of the *Centaurio-Saginetum* originate from such sites e.g. Westhoff (1947) and also the original one: Diemont *et al.* (1940).

The other species of the third group in Table 1 belong to the related association: *Sagineto maritimae-Cochlearietum danicae* (Tx. 1937) Tüxen et Gillner 1957. This plant community occurs in the ecotone between the xerosere and the halosere. It is composed of annuals and biennials like *Sagina maritima*, *Cochlearia danica* and *Parapholis strigosa*. All the characteristic species of this community prefer a fluctuating water content and salinity of the soil. They establish themselves on open patches within plant communities of the *Armerion*-alliance, which they cover as a 'carpet' (Teppich-Gesellschaft sensu

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[1]) Data of elevation are based on a few measurements only.

[2]) The author prefers the name *Centaurium vulgare* Rafn to *Centaurium littorale* (Turner) Gilmour, which was used in a previous paper. The latter is also used in some modern Westeuropean floras. However the only correct name is Centaurium vulgare Rafn as is discussed by Jonker (1950).

TABLE 1

Name of association	Centaurio-Saginetum					Sagino-Cochlearietum					Juncetum gerardii				
No. of column	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
No. of analysis	47	2	10	5	4	S48	56	S7	S12	M5	54	B5	B2	B4	B1
Total cover in %	90	75	40	60	70	60	30	80	95	60	85	100	100	100	100
Moss cover in %	5	25	0	5	5	10	0	20	15	30	10	0	0	0	0
Area in m²	2 × 2	2 × 2	2 × 2	2 × 2	2 × 2	½ × ½	2 × 2	1 × 1	½ × ½	2 × 1	4	1 × 1	1 × 1	1 × 1	1 × 1
Other dune plants	5	.	.	1	.										
Sonchus arvensis	.	.	*x*.1	.	.		*r*								
Eryngium maritimum	.	.	.	*x*.1	.		*r*								
Hieracium umbellatum	*r*	.	*r*	.	.										
Poa pratensis	1.2	1.2		.	.										
Calamagrostis epigejos	.	1.1	.	.	1.1										
Anthyllis vulneraria	.	1.1	.	2.2	.	.	.	.	.	*x*.1					
Cerastium semidecandrum	1.1	*r*	.	.	*r*	.	2.1	.	.	.					
Sedum acre	*x*.2	.	1.1	2.2	2.2	.	1.1	1.2	.	1.2					
Leontodon nudicaulis	*r*	*x*.1	*x*.1	*x*.1	*r*	.	1.2	.	1.1	.					
Cerastium atrovirens	1.1	1.1	1.1	2.1	2.1	2.2	2.1	1.1	1.1	1.2					
Festuca arenaria	3.3	4.3	2.2	3.4	4.4	2.2	2.2	2.2	2.2	3.3					
Cochlearia danica	*x*.1	*x*.1	2.1	1.1	1.1	*x*.1	1.2	*x*.1	*x*.1	*x*.1					
Centaurium vulgare	1.2	2.2	2.1	1.1	1.1	*x*.2	1.1	3.2	1.1	1.1					
Sagina nodosa monilif.	*x*.2	1.2	1.1	1.1	1.2	.	1.2	.	*x*.1	1.1					
Sagina maritima	1.3	1.2	*x*.1	1.1	1.1	1.1	1.2	2.2	3.2	2.1					

Name of association	Centaurio-Saginetum					Sagino-Cochlearietum					Juncetum gerardii				
Plantago coronopus	.	.	*r*	*x*.1	*r*	3.2	.	.	1.1	.					
Parapholis strigosa	.	.	*r*	.	.	.	1.1	1.1	1.1	*r*					
Pottia heimii	.	.	.	.	.	1.2	.	2.2	1.2	.					
Festuca litoralis	*x*.1	1.2	2.2	.	*x*.2	.	*x*.2	2.2	2.2	1.3	*x*.2	4.5	5.5	5.5	5.5
Agrostis salina	1.2	1.2	1.2	1.2	1.2	3.2	1.2	2.1	1.2	*x*.2	4.2	1.2	2.2	2.2	2.2
Juncus gerardii	.	.	.	.	.	.	.	.	.	.	2.3	4.5	.	.	.
Plantago maritima	*r*	.	*r*	*x*.1	*r*	.	*r*	*x*.1	.	*x*.1	*x*.1	*x*.2	1.1	*x*.1	1.1
Limonium vulgare	.	.	.	*r*	1.1	.	*r*	*x*.1	*x*.1	1.1	*x*.1	*x*.1	1.1	*x*.1	1.1
Euphrasia odontites . . .	*r*	.	*r*	.	*r*	.	*r*	*x*.1	.	1.1	1.2	.	*x*.1	*r*	*r*
Armeria maritima	.	*x*.1	.	*x*.1	*x*.1	.		3.2	3.2	1.2	.	.	1.2	*x*.1	1.1
Elytrigia pungens	.	*r*	.	*x*.1	*x*.1	1.1	*r*	.	1.2	*x*.1	.	.	1.2	.	.
Halimione pedunculata . .	.	.	.	*r*	*r*	*x*.1	*r*	*x*.1	.	*r*	*r*	.	.	.	.
Glaux maritima						.	.	.	*x*.1	*x*.1	1.2	3.2	.	*x*.1	1.1
Centaurium pulchellum . .						.	*r*	.	*x*.1	*x*.1	2.2	.	.	*r*	*x*.1
Carex extensa						.	.	.	1.2	*r*	*x*.2	*x*.2	.	*r*	*x*.1
Triglochin maritima . . .						.	.	.	*x*.2	.	.	*x*.1	*x*.1	1.1	*x*.1
Cochlearia anglica						.	.	.	.	.	.	.	*x*.1	.	*r*
Spergularia marginata . .						.	.	*x*.1	.	.	*r*	.	.	.	.
Artemisia maritima						.	.	*x*.1	.	*r*	.	.	.	.	.
Other halophytes						.	1	.	.	.	1	.	1	.	.

Addenda: column 1: Ammophila arenaria 1.1, Aira praecox 1.1, Hippophaë rhamnoïdes r, Linum catharticum 1.2, Taraxacum spec. r; column 5: Trifolium repens r; column 7: Juncus articulatus r; column 11: Carex distans r; column 13: Trif. fragiferum *x*.1.

Location: 2 and S48 in 'Eerste Duintjes', 47 and 54 in 'Tweede Duintjes', other analyses on horseshoe dunes.

Authors: S48, S7 and S12 by J. Spekman and J. Groten; B5–1 by Miss H. T. A. van Heusden; all other analyses by the present author.

Tüxen). Many papers have been published on the *Sagino-Cochlearietum* in recent years: Beeftink (1965), Tüxen and Westhoff (1963), Spekman and Groten (1963), Westhoff *et al.* (1962) and Tüxen (1957).

The relationship between the *Centaurio-Saginetum* and the *Sagino-Cochlearietum* is strong. It is difficult to make a sharp distinction between the two on the Boschplaat. In general it can be said, that *Centaurium vulgare* and *Sagina nodosa* prefer a somewhat drier and less saline soil than the species of the *Sagino-Cochlearietum.* This explains why *Cochlearia danica* – typical for the dry subassociation *sedetosum* of the *Sagino-Cochlearietum* possesses a high vitality in the *Centaurio-Saginetum.* In view of the strong ecological similarity of the *Centaurio-Saginetum* and the *Sagino-Cochlearietum* the characteristic species of these two communities were combined in Table 1 and discussed here together. A more detailed description of both communities on the Boschplaat and their mutual relations will be published in the future.

On the horseshoe dunes the open vegetations of the *Centaurio-Saginetum* suddenly pass into the very closed sward of *Festuca rubra f. litoralis* Hackel. The last five columns of Table 1 give an impression of the plant community, in which this paramorph of *Festuca rubra* dominates. Apart from the most important species, *Festuca litoralis*, two other species can dominate, viz. *Agrostis stolonifere subvar. salina* Jansen et Wachter 1940 and *Juncus gerardii* (cf. Van Heusden, 1963). The former occurs especially in the brackish slacks of the "Duintjes" (column 11) and the latter on more wet places (column 12). The old name for this community is: *Armerieto-Festucetum* (W. 1890) Braun-Blanquet et de Leeuw 1936. Beeftink (1965) uses the name: *Juncetum gerardii* Warming 1906. This author distinguishes three variants with dominance of respectively *Festuca litoralis*, *Agrostis salina* and *Juncus gerardii.*

These three variants were observed on the Boschplaat too as was already suggested. In the *Juncetum gerardii* a number of other halophytes, mostly with a low abundance and vitality are found. Dune plants do not occur within it as a consequence of the high density of the vegetation and the soil properties. The lower limit of the *Juncetum* corresponds with the spring tide level = 127 cm + N.A.P.

The columns 5 to 10 represent the *Sagino-Cochlearietum* of the Boschplaat. The most essential features of this community were already described above. We can subjoin the following remarks. As in the case of the *Centaurio-Saginetum* there are the two opposite groups of dune plants and halophytes. Differing from the *Centaurio-Saginetum* the accent lies on the halophytes. The two paramorphs of *Festuca rubra* are in balance. The community is typified by the occurrence of *Sagina maritima*, *Plantago coronopus*, *Parapholis strigosa* and *Pottia heimii*, the vitality of *Sagina maritima* is better than in the *Centaurio-Saginetum*, but on the other hand *Centaurium vulgare* and *Sagina nodosa* form much smaller plants in the *Sagino-Cochlearietum.* As is told above the *Sagino-Cochlearietum* develops on open spots of other vegetations.

In our case these open spots lie in the *Juncetum gerardii*. There they arise by erosion during gale-floods and also as a consequence of the combined influence of dryness and a high salt concentration on the original vegetation. Maybe flood marks play a part. The lower limit of the *Sagino-Cochlearietum* on the horseshoe dunes is about 137 cm + N.A.P.

3. THE SOIL

The soil surface in the *Juncetum gerardii* is covered by a thick layer of dead organic material. Its decomposition takes much time. The upper layer of the mineral soil, about 5 cm, contains 4% silt and clay.

The soil surface of the *Sagino-Cochlearietum* is coated with algae especially *Cyanophyceae*, among others *Nostoc microscopicum*. The substratum for these algae is formed by the silty top layer of the soil. The approximately 1 cm thick layer contains up to 6% silt and 3% organic material.

Contrary to the two just described soils, the soil of the *Centaurio-Saginetum* is almost completely sandy. The amount of humus is negligible. Algae are present but barely visible. However, these few algae are responsible for the formation of a crust-hard soil surface during spells of dry weather. Both the algae and crystallized salts cement the sand grains together.

TABLE 2

Association	Cent.-Sag.		Sag.-Cochl.		Junc. ger.	
soil layer in cm.	0–1	1–20	0–1	1–20	0–5	5–20
max. H_2O–%. . .	10.8	16.0	31.9	18.6	213.9	30.4
min. H_2O–%. . .	0.2	2.3	0.7	3.6	53.9	15.1
max. Cl′–%. . .	(1.20)	0.10	(0.59)	0.09	0.61	0.44
min. Cl′–%. . .	0.02	0.02	0.01	0.01	0.02	0.05

All figures are based on twelve fortnightly samplings in 1964, H_2O-content in % of dry soil and Cl′-content as concentration of soil moisture. For method and for comparison, see FREIJSEN (1964).

Table 2 gives a survey of the water relations and the salinity in the communities studied. From left to right in Table 2 the water content and the salinity increase. The superficial layers of the *Sagino-Cochlearietum* and the *Juncetum gerardii* can contain a high amount of water. The layer of 5–20 cm in the latter association is permanently saturated with water because of a high phreatic level. The minimum water content in the *Centaurio-Saginetum* and the *Sagino-Cochlearietum* can be very low. Especially the surface of the soil in these associations can desiccate strongly.

The Cl′-concentrations in the *Centaurio-Saginetum* and the *Sagino-Cochlearietum* are almost the same, but the absolute amount of Cl-ions (= potential salinity sensu ADRIANI in: WESTHOFF *et al.*, 1962) is higher in the *Sagino-Cochlearietum*. This absolute amount is higher, but also the moisture content in the latter is higher as well, resulting in a Cl′-concentration, which is the same as in the *Centaurio-Saginetum*.

The situation in the *Juncetum gerardii* is quite different. A higher degree of salinity goes with a permanently wet soil. The *Juncetum gerardii* is a true salt community. The two maximum Cl′ figures of the topmost layers of the *Centaurio-Saginetum* and *Sagino-Cochlearietum* are placed between brackets. It is questionable, whether such high values really exist. According to BEEFTINK (1965) crystallization must happen under these circumstances.

Other soil factors differ only slightly and probably do not determine the boundaries of the three associations. The only remarkable feature is a somewhat greater richness of nutrients in the 0–4 cm layer of the *Juncetum gerardii*.

4. THE FIELD PLOTS

Introduction

The previous parts render a short survey of the most important plant communities on the Boschplaat between the levels of stormflood and spring tide. Secondly the critical soil factors in these habitats are summarized. In order to get an idea about the origin of this ecotone, five field plots were laid out, transverse to the zonation. By digging up the soil and removing the original vegetation and a part of the grass roots, bare sandy plots were prepared. The cover of algae and silt disappeared and so the soil material was about identical throughout the fields. (In two other field plots – not mentioned here – the lower part was filled with sand from high on the dune slope. The results of these two fields correspond with the following remarks and conclusions.) Only the water relations must have been different from the starting point as a consequence of the gradient in the water-table. This was also the case with the Cl′-concentration, which depends upon the soil moisture.

Table 3 renders the details about number, data of laying-out and last inspection and size of the five field plots. The plots 1, 2 and 3 were laid out on west slopes of horseshoe dunes with distinct zones; plots 4 and 5 were situated in respectively the ‘Eerste Duintjes’ and ‘Tweede Duintjes’. As was told in part 1, the *Juncetum* of the ‘Duintjes’ is characterized by a low salinity and the dominance of *Agrostis stolonifera salina*. This difference appeared in the development of field plots 4 and 5.

To make sure the establishment of *Centaurium vulgare* in the field plots, for which phenomenon much interest existed (see part 4), all field plots, except no 5, were sown with seed of *Centaurium vulgare*, collected on the Boschplaat.

Discussion of Table 3

Table 3 renders a survey of all species which established themselves on the field plots within the period between the laying-out and the last inspection. As far as possible they are placed in the same order as in Table 1. For this investigation a period of one year was chosen so that plants normally germinating in spring as well as plants germinating in autumn should have at least one opportunity to germinate. In Table 3 the presence of a species after one year is designated by the symbol +; the absence by the symbol —. Species only one time occurring on all fields together are joined as 'other dune plants' and 'other halophytes'.

TABLE 3

o. of field plot	1	2	3	4	5
ate of laying-out	Apr. 1964	Nov. 1962	Nov. 1962	Aug. 1962	Aug. 1962
ate of last inspection	Jun. 1965	Oct. 1963	Oct. 1963	Jul. 1963	Oct. 1963
ze in m²	10 × 2,5	6 × 1,25	6 × 1,25	3 × 2	3 × 2
dry half of field plot:					
ther dune plants	3	0	0	0	2
lytrigia juncea	+	+	+	—	—
rifolium repens	+	+	+	—	—
otus corn. ssp. corniculatus	+	—	—	+	—
onchus arvensis	+	+	+	—	+
oa pratensis	+	—	—	+	—
erastium semidecandrum	—	—	—	+	+
edum acre	+	+	+	+	+
eontodon nudicaulis	+	—	+	+	+
erastium atrovirens	+	+	+	+	+
estuca rubra v. arenaria	+	+	+	+	+
ochlearia danica	+	+	+	+	+
wet half of field plot:					
entaurium vulgare	+	+	+	+	+
agina nodosa v. moniliform.	+	+	+	+	+
agina maritima	+	+	+	+	—
lantago coronopus	+	+	—	—	—
estuca rubra f. litoralis	+	+	+	+	—
grostis stolon. v. salina	+	+	+	+	+
imonium vulgare	+	+	+	—	—
uphrasia odontites	+	+	—	—	—
rmeria maritima	+	—	+	+	—
alimione pedunculata	+	+	+	—	—
laux maritima	+	+	+	+	—
entaurium pulchellum	+	+	+	—	—
ochlearia anglica	+	+	—	+	—
otentilla anserina	+	—	—	+	—
ther halophytes	1	3	1	0	0
Throughout the field plot:					
lantago maritima	+	+	+	—	—
lytrigia pungens	+	+	+	—	—
rtemisia maritima	+	+	+	—	—
triplex hastata	+	—	—	—	—
otal number of plants	32	25	22	17	12

The species in Table 3 are divided into three groups:

a. the first group consisting of xerophile species occurring only or especially on the upper dry half of the field plots,
b. a second group of relatively hydrophilous species mostly occurring on the wet lower half of the field plots,
c. a third group of a few species which occurred throughout the field plots with similar abundance.

After a year the most important *Koelerion*-species of Table 1 had established themselves on the upper half of the field plots. In many respects the original composition and structure of the vegetation was restored. A conspicuous difference was formed by *Sonchus arvensis* and *Elytrigia juncea*. Both psammophile plants were apparently favoured by the loose sandy surface in the upper part of the plots. Interesting was the preference of *Cochlearia danica* to the dry half of the plots. In this way the mentioned xerophile character of this *Sagino-Cochlearietum* species appeared.

The species in the first group of Table 3 did almost not establish themselves in the wet half of the plots which corresponded with the *Juncetum gerardii*. This was unexpected as some disadvantageous features were absent, e.g.: a high density of the vegetation, a thick layer of litter, and a higher silt content. The conclusion must be that the lower limit of these species on the Boschplaat is determined by the water and salt content of the soil. These must be the main reasons that they do no occur in the *Juncetum gerardii* and that they possess a lower vitality in the *Sagino-Cochlearietum*. Indeed they are oligohygrobious and oligohalobious plants sensu IVERSEN (1936).

Among the species of the wet lower halfs of the field plots there are many halophytes mentioned as such in Table 1. With regard to the factors water and salt these species behaved oppositely to those of the *Koelerion*. Shortness of water and salt were the causes that the true halophytes of the *Juncetum gerardii* did not reach a high abundance or dominance on the level of the *Centaurio-Saginetum*. The species of the wet halfs of the plots are mesohygrobious and mesohalobious (IVERSEN, 1936). The number of these species is much lower in the field plots 4 and 5. In field plot 5 *Agrostis salina* is the only 'halophyte'. The more fresh character of the environment – the slacks of the 'Duintjes' – must be the cause.

Four species of the two associations *Centaurio-Saginetum* and *Sagino-Cochlearietum* exhibit another trend: *Centaurium vulgare*, *Sagina nodosa* var. *moniliformis*, *Sagina maritima* and *Plantago coronopus*. Their area in the field plots was restricted to the lower half contrary to the normal situation. The upper boundary for the plants of *Centaurium vulgare* and *Sagina nodosa* was below the boundary line between the *Centaurio-Saginetum* and the *Juncetum gerardii* in the surrounding vegetation. This upper boundary – normally occurring on the level of the storm-flood mark – was shifted downwards. On the field plots the *Centaurio-Saginetum* did not occur, but coincided with the 'community' of *Sagina maritima*.

The following explanation is possible. *Centaurium* and the other species prefer rather wet soils especially during germination. However the soil surface in the upper halfs of the field plots was dry and loose. Furthermore favourable microhabitats were nearly absent as a consequence of the particular preparation of the field plots. Recently Harper *et al.* (1965) have shown the importance of the 'microtopography' for germination. In the undisturbed *Centaurio-Saginetum* – on the same elevation as the dry halfs of the field plots – enough microhabitats occur. In the wet halfs of the plots germination happened especially below drift material, in the shadow of small tussocks etc. The microrelief appeared to be important here too.

After some time the species of the *Sagino-Cochlearietum* seemed to be superseded by the dominant growth of grasses, especially *Agrostis stolonifera salina*, and *Festuca rubra litoralis*. This development was prohibited by removing the stolons of the grasses. Also under natural conditions the *Sagino-Cochlearietum* can be succeeded by the *Juncetum gerardii*, in which succession the constructive capacities of the grasses are of major value. The grasses increase the density of the vegetation. This process is favourable for the sedimentation of silt, but unfavourable for the occurrence of the pioneer plants of the *Sagino-Cochlearietum*. Thus a *Juncetum*-community develops. Some of the species of the *Sagino-Cochlearietum* can find a refuge on a higher level, namely in the *Centaurio-Saginetum* e.g. *Sagina nodosa* and *Plantago coronopus*.

In the third group of Table 3 four plants occur, which possessed the same abundance throughout the field plots 1, 2 and 3. Their diaspores were conveyed in the tidal drift. The plants themselves profited of the presence of the organic material. Especially *Elytrigia pungens* and *Atriplex hastata* are found on places, where tidal drift is deposited on the salt marsh. These four species were not found on the field plots 4 and 5 in the slacks of the 'Duintjes'. These dunes are inundated some times a year, but the quantity of deposited tidal drift is extremely low. The absence of these four species mentioned and of many halophytes caused the low total number of plants on these fields.

5. CENTAURIUM VULGARE RAFN

During the investigations on the field plots special attention was given to *Centaurium vulgare* Rafn. This species has some paramorphs described by Jonker (1950) and also by other authors. On the Boschplaat the typical *Centaurium vulgare* occurs. Normal adult specimens of this paramorph are characterized by a number of branched erect stems, narrow somewhat succulent leaves and purple-rose flowers. Their rosettes die off after the winter.

It was the purpose to get information about the life-history and the distribution of this paramorph of *Centaurium* in the zone between the levels of storm-flood and spring tide. In order to be sure that *Centaurium vulgare* should occur, seeds of this species were sown on the field plots, as well as on two control plots in the natural vegetation alongside the plots 2 and 3. As was mentioned in a previous section, *Centaurium vulgare* established itself only in the lower part of the field plots, always below the boundary line between the xerosere and the halosere.

The life-cycle

About the life-cycle of *Centaurium vulgare* the following can be said. On 20 May 1963, not a single seedling was found on the field plots 2 to 5. In the surrounding vegetation the first seedlings were already found in April. The cause of this delay of germination has not been cleared yet. During their first summer the seedlings developed in rosettes. The plants hibernated as rosettes and after exactly one year they formed stems. They flowered in July and August of the second summer. After the leaves and stems had turned yellow the plants formed seeds. These plants behaved as true biennials as is the normal way for *Centaurium vulgare.*

The distribution pattern in field plot 2

The distribution of *Centaurium vulgare* in the field plots can be explained in a description of the occurrence of *Centaurium vulgare* in field plot number 2. In this respect field plot 2 was representative for all plots.

On 31 July 1964 – in the flowering-time of *Centaurium vulgare* – size and density of the specimens of *Centaurium vulgare* on plot 2 were measured. Table 4 contains the results of this investigation. First there is a longitudinal profile on scale of the lower half of field plot 2, which corresponds with the *Juncetum gerardii.* As mentioned above *Centaurium vulgare* occurred only in this part of the field plot. This half was subdivided in five subplots of 35 × 135 cm^2. In each subplot the following properties of *Centaurium vulgare* were determined:

a. the total number of plants
b. the maximum length of the stems
c. the average number of flowers per plant
d. the average number of stems per plant
e. the average dry weight in g per plant.

No plant of *Centaurium vulgare* occurred in subplot 1. The first specimens were found in subplot 2, 10 cm below the boundary line between the *Centaurio-Saginetum* and the *Juncetum.* The subplots 3 and 4 possessed the highest density of specimens of *Centaurium vulgare.* Above and below these two patches the density decreased. Going down the slope the length of the stems decreased. The decreasing size of the plants on the slope was more clearly shown by the diminishing number of flowers from 70 to 8 per plant in the subplots 2 to 5. Normally each flower produces a fruit. From other investigations it appeared that big plants use to produce more seeds per fruit. So it is allowed to conclude, that the seed production in the highest subplots was much higher than below, at least per plant.

The same tendency – decreasing vitality of the plants in the lower subplots – appears from the data about the average number of stems and the average dry weight.

It can be supposed that the lower half of field plot 2 – in which *Centaurium vulgare* growed – possessed a high homogeneity. At the start of the experiment the environment was the same throughout the field plot. An exception was formed by the soil moisture which increased going down the slope. Hence the changing water content of the soil must be the cause of the distribution pattern of *Centaurium vulgare*.

Three zones could be discerned in the "*Centaurietum*" of field plot 2:

1. upper zone with few big plants of *Centaurium vulgare* = subplot 2
2. middle zone with highest density and rather small plants = subplot 3 and 4
3. lower zone with few and very small plants = subplot 5.

DISCUSSION

The relation between the distribution pattern of *Centaurium vulgare* and the soil moisture can be explained as follows. On the top of a sandy dune slope the soil water becomes the limiting factor for *Centaurium vulgare*. For germination the water content only suffices on a few places e.g. pores in the soil surface or shadowing tussocks etc. (see above). The density of seedlings is always low. These dispersed seedlings exhibit a rapid growth. Their roots become soon long enough to reach a depth with sufficient capillary water.

Somewhat lower on the same dune slope the surface is wetted by capillary rise from the water-table during spring. Here the water factor is no more limiting the germination. That's why the number of seedlings of *Centaurium vulgare* is much higher. The density of the rosettes and later the adult plants, which develop from the seedlings, is so high that they exhibit a negative influence on each other. This phenomenon must be an example of competition within one species. We can say that density is inversely proportional to size and production of the individual plants of *Centaurium vulgare*.

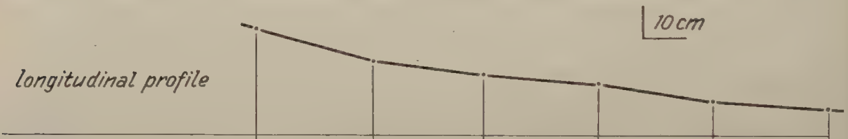
The competition of *Centaurium vulgare* resembles that observed by BLEASDALE (1960) and HARPER (1960) in their studies with weeds. The amounts of water and light can not be in short supply. As we have seen, the soil moisture is high in the middle part of the *Centaurium*-zone. Also in dense *Centaurium*-populations the amount of light is always sufficient. Their density and height is not high enough to hinder the penetration of the light. Thus a shortness of nutrients must be the limiting factor. The rightness of this conclusion was proved by an experiment with fertilizers. The size of the *Centaurium*-plants in dense populations increased after supply with fertilizer.

On the lower edge of dune slopes the permanently high content of soil moisture becomes increasingly unfavourable for *Centaurium vulgare*. The presence of a coating of algae – as a consequence of the high humidity – may be disadvantageous too. The number of seedlings is low and becomes still lower by mortality. In spite of the wide interspaces between the individual plants, which makes competition for nutrients very improbable, they grow slowly and the adult plants attain only a small size.

The different size and density of *Centaurium vulgare* on high and low levels of dune slopes use to occur in natural vegetations too. *Centaurium vulgare* possesses big specimens and a low density in the *Centaurio-Saginetum* of the Boschplaat. On the other hand, in the *Sagino-Cochlearietum* we meet many rather small specimens. The columns 2 and 3 in Table 4 symbolize these two situations in the behaviour of *Centaurium vulgare*.

TABLE 4

Size and density of *Centaurium vulgare* in the lower half of field plot 2



subplots no.	1	2	3	4	5
total no. of plants	0	23	52	38	20
max. length of plants (cm)	–	30	23	22	18
no. of flowers per plant	–	70	21	11	8
no. of stems per plant	–	8	3	2	1
gr. dry weight per plant	–	7,4	2,8	1,4	0,7

Finally the following remarks can be made with reference to the field plots. First it is peculiar that there were almost no seedlings of *Centaurium vulgare* on them in the second season after their laying-out. It can be concluded that there was just a very low amount of viable seeds. Either the original seed had germinated, or it had lost its germinative power. New seed was not conveyed from the neighbourhood, although there were enough seed producing plants. The conclusion must be that, as a rule, the seeds of *Centaurium vulgare* are dispersed over small distances only. This conclusion is in accordance with observations in a very young dune region of Terschelling: the 'Noordvaarder'. There the area of *Centaurium vulgare* does not extend to its possible limits. The expansion of *Centaurium vulgare* is slower than the development of new habitats. That is: the dispersal of *Centaurium vulgare* is a limiting factor for the rate of extension of its range.

In spite of sowing the density and distribution of *Centaurium vulgare* in the two control plots was quite the same as under natural circumstances. No plants occurred in the *Juncetum gerardii* of these plots. In this respect the behaviour of *Centaurium vulgare* was not influenced by sowing, just as was expected.

The biomass of *Centaurium vulgare* on field plot 2 (see Table 4) was significantly higher than on an area of the same size in a natural habitat. Also other plants attained a larger size. Without doubt this phenomenon is a result of a higher amount of easily available nutrients, because the soil had been dug up.

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CYTOTAXONOMIC STUDIES IN CARDAMINE PRATENSIS L. IN THE NETHERLANDS

C. C. BERG

(*Botanical Museum and Herbarium, Utrecht*)

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Abstract

In material of *Cardamine pratensis* from many localities in the Netherlands, the following somatic chromosome numbers were counted: 28, 30, 31, 32, 34, 36, 38, 39, 45, 46, 52, 53, 54, 56, 58, 59, 60, 62, 64, 64 à 66, 67, 68, 69, 70, 72, 73, 74, 75, 76, 78, (80), 84, and (118) [1]. Many numbers were due to intra-individual deviation of the normal number. As main groups tetraploids with 28–32, octoploids with 56–64, and decaploids with 70–80 chromosomes could be distinguished; the normal numbers of the ploidy levels were 30, 60, and 74–76, respectively. Two subspecies could be distinguished on the basis of morphological, ecological, and cytological characters.

Introduction

In the morphologically and ecologically very variable species *Cardamine pratensis* L. a large number of cytotypes has become known from many countries. In most cases only one or a few individuals were examined. In investigations by Banach (1951), Hussein (1955), and Lövkvist (1947, 1956) a larger number of individuals was involved. Moreover, Banach studied the cytological differentiation in connection with ecology, and Lövkvist in connection with morphology, ecology, and distribution, completed with crossing experiments. These studies showed regional differences in the cytological differentiation of *C. pratensis*.

Lövkvist (1956) distinguished in the temperature zone of Europa 6 species in the *C. pratensis* complex. Only *C. pratensis* L. s. str. and *C. palustris* Petermann could be expected in the Netherlands. These species could be distinguished cytologically, ecologically, and morphologically; moreover, restrictions in compatibility were evident. In *C. pratensis* L. s. str. common chromosome numbers were 16, 30, and 44 (being at the di-, tetra-, and hexaploid level, respectively). Chromosome numbers of *C. palustris* Petermann proved to be 56 or higher (being at the octo-, deca-, and dodecaploid level). There are indications that the two taxa cannot be separated satisfactorily in all parts of the distribution area, while the morphological discontinuity does not always appear to be correlated with the same ploidy level (see Schulz, 1903; Lindman, 1914; Banach, 1951; Hussein, 1955; Lövkvist, 1956; Clapham, Tutin and Warburg, 1962).

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[1] Numbers in parentheses could not be determined exactly.

A positive correlation between the chromosome number and the water content of the substrate was evident (Banach, 1951; Lövkvist, 1956).

The primary object of this study was to get some impression of the cytological differentiation of *C. pratensis* in the Netherlands and to investigate if and how the above mentioned taxa could be distinguished.

Material and methods

From several parts of the Netherlands one or some individuals from a population were collected. Most of them were grown in experimental gardens. Chromosome counts were made on metaphase plates of roottip cells. The roottips were fixed in Karpechenko, embedded in paraffin, sectioned at 15 μ, and stained according Heidenhain's haematoxylin method. In each preparation at least 3 metaphase plates were examined. Voucher specimens of the investigated plants have been deposited in the Herbarium of the State University of Utrecht.

Cytologycal results

The plants often showed intra-individual variation of the chromosome number, usually within the limits of the ploidy level (see Lövkvist, 1956). In most of these plants, however, one or possibly 2 numbers can be considered to be the normal numbers of the ploidy level, as they are usually present in the plant or within the population.

The following somatic chromosome numbers were counted, as the only number found in the plant or together with other numbers: 28, 30, 31, 32, 34, 36, 38, 39, 45, 46, 52, 53, 54, 56, 58, 59, 60, 62, 64, 64 à 66, 67, 68, 69, 70, 72, 73, 74, 76, 78, (80) [1]), 84, and (118).

Tetraploids (**2*n* = 28–32**)

30 was counted in plants from about 50 localities; it is the normal number at this ploidy level and the commonest one in *C. pratensis* L. s.l. in the Netherlands. 28 was found three times together with 30 and/or 32; 31 twice, and 32 fourteen times as the only number or together with other numbers at this level. There were indications that the numbers 31 and 32 had been caused by chromosome fragmentation. Sometimes 60 or c. 60 has been found as an endopolyploid number.

Octoploids (**2*n* = 56–64**)

Octoploids are known from 4 localities listed in Table 1. They always occurred together with tetraploids and sometimes with decaploids, too. 60 appeared to be the normal number at the octoploid level. This number usually occurred together with other numbers

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[1]) Numbers in parentheses could not be determined exactly.

Table 1

Origin of the material and collection numbers	Somatic chr. numbers [1])
Monnikendam: 483C, 487C	30
489	32
475	36, 38
476	38
487E	45
478	46, (45)
482	52, 53
479, 481, 483D	60
484, 486D	68
485B	67, 68, 69
486C	72, 73, 74
480	74, 76, (72)
Between Keizersveer and Sleewijk: 429, 431, 433, 436, 437	30
432	28, 30, 32
435	32
430, 434A, 434B, 438	68
Meerkerk: 439	34, 36, 39
440	74, 76, 78, (68)
Brabantse Biesbos near Drimmelen:	
425, 526, 495, 498, 503F, 507B	30
500	28, 30, 32
494	58
496	58, 60, 64, (118)
505C	60, 62, (58)
499D	59, 60, 62, 64
502B	56, 64
503A	60, 62, (64)
Near Ulvenhout, loc. I: 414, 415, 416	30
413	32
loc. II: 418	30
417, 419	30, 31, 32
Near Bavel: 420, 421, 422, 423	30
424	60
Near Etten-Leur: 402, 407, 408, 505D, 506	30
403, 405, 504	74
411, 415	76
404, 511	72, 74, 78, (68)
410	74, 78
406	54, 84
Near Terheyden (N.B.): 398	30
401	32
399, 400	76
Near Oostvoorne: 253–255, 258–260, 266–268	30
256, 257	32
445B	64, 68
445G	68
445H	64 à 66
445I	68, 72, (64)
446A	58, 60, 62
446D	59, 60, 62
446E	60, 62, (58), (64)
Near Rockanje: 263, 264, 448	30
447E	68, 70, 74, 76
447A	70, 76
Near Kortenhoef: 452A, 452B	74, 76, 78
454A, 454B	76

[1]) Numbers in parentheses could not be determined exactly.

of this level, although in some plants 60 could not be found. Once c. 118 was found as an endopolyploid number.

Decaploids ($2n = 70–80$)

Decaploids were met with in 13 localities besides those mentioned in Table 1 near Utrecht, Westbroek, Eemnes, Lemmer, Oosterhout (N.B.), and Heelsum. 74 and 76 appeared to be the normal numbers; these numbers could occur together and/or in combination with other numbers at this level. Once 75 was counted as the only number.

Other chromosome numbers

In populations with decaploids plants were found with 34 and 36, or 38, or 36, 38, and 39 chromosomes. Plants with 45 or 46 chromosomes were met with together with tetraploids and octoploids; one plant with 52 and 53 chromosomes in a population with tetraploids and decaploids.

68 chromosomes were counted in individuals originating from some neighbouring localities, probably in pure breeding populations. The number of 68 occurred once together with numbers at the decaploid level.

68 chromosomes were also found to occur in combination with other numbers in plants originating from populations containing octoploids or decaploids and octoploids.

54 chromosomes were once found in a preparation in which all other counted metaphase plates showed the number $2n = 84$.

When roottips of the same plant were fixed at different moments, it often appeared that one preparation showed, e.g., only 32 chromosomes and the other only 30, or that the one appeared to have a varying chromosome number at the decaploid level, while in the other, for instance, only 76 were counted.

Table 1 gives a selected list of chromosome counts, with indication of the origin of the plants and their collection numbers.

Crossing experiments

Some crossings were made between plants of different ploidy levels. The results were partly investigated and appeared to be very confusing. In the framework of this publication should be mentioned that plants with c. 68 chromosomes were obtained from crossings between octoploids and decaploids and an individual with c. 45 chromosomes from a crossing between a tetraploid and an octoploid.

Restrictions in compatibility between octoploids and decaploids on the one and tetraploids on the other side appeared to be more or less evident.

DISCUSSION

The somatic chromosome numbers counted by several workers up to 1956 are, according to tables given by LÖVKVIST (1956): 16, 28, 30, 32, 33, 34, 37, 38, 40, 43, 44, 45, 46, 48, 50, 52, 54–68, 70–78, 80, 84, 88, > 90, and c. 96. Other chromosome numbers were not known so far. New numbers obtained from the present study are 31, 36, 39, 53, 69.

8 is the basic number in *Cardamine*. According to Lövkvist (1956, 1963) 7 may be conceived as a second basic number. Combinations of these numbers can theoretically give several euploids at the each ploidy level (e.g. at the octoploid level 56, 58, 60, 62, and 64). This classification, suggested on account of chromosome numbers in *Cardamine* and the distribution of longer chromosomes in the cytotypes of *Cardamine pratensis*, has been taken over in this study, although not for the same reasons.

The presence of intra-individually variable chromosome numbers, called aneusomaty (Duncan, 1945), in tetra-, octo-, and decaploids, is a remarkable phenomenon which formerly was not known in *C. pratensis*. It might be caused by chromosome fragmentation and chromosome deletion. The latter possibility was suggested by Lövkvist (1956) for aberrant chromosome numbers in pure breeding populations of a high ploidy level. The possibility of chromosome fusion was also pronounced (Lawrence, 1931; Lövkvist, 1963).

Lövkvist (1956) regarded as pure breeding populations in the South of Sweden and Danmark those with $2n = 30$, (38), 56, (60), 64, 68, 72, 76, 80 and c. 96. In general most other numbers would have been caused by hybridization. In the Netherlands pure breeding populations with $2n = 30$, 60, 68 and 74–76 appeared to occur. The number of hybrids seems to be rather small. In the British Isles 30 and 56 are common somatic chromosome numbers, while 32, 38, 48, 57, 58, 64 and 72 have been counted incidentally (Hussein, 1955; Lövkvist, 1956). In Poland 30, 32, 44, 50, 58, 64, 72, 76 and 78 have been counted (Banach, 1951). Thus the cytological differentiation in *C. pratensis* in the Netherlands appears to differ more or less from that of other regions where tetraploids, octoploids, and decaploids occur.

As plants of each ploidy level showed aneusomaty, it is conceivable that these levels are connected by autoploidization. The distribution of the octoploids indicated the possibility that they are autoploids of tetraploids.

Plants with chromosome numbers between 32 and 40 might be subhaploid developments from octoploids or decaploids, as already suggested by Lövkvist (1956).

Individuals with $2n = 45$–46 and 52–53 probably are hybrids of tetraploids on the one side and octoploids or decaploids on the other side, whereas those with 68 or c. 68 chromosomes may be hybrids of octoploids and decaploids.

Morphology

Several characters have been studied to find differences between octoploids and decaploids on the one side and tetraploids on the other. Table 2 gives some more or less useful differentiating characters.

In most cases the characters of the uppermost cauline leaves are sufficient to distinguish both groups. It was impossible to distinguish octoploids from decaploids. Plants with chromosome numbers between the tetraploid level and the octoploid level mostly resembled the tetraploids.

In general these results confirm those of LÖVKVIST (1956).

TABLE 2

Characters	Octoploids and decaploids	Tetraploids
uppermost cauline leaves	pinnate; leaflets, except the terminal one, deciduous	pinnatifid
lateral racemes	mostly absent or few	mostly present and more numerous
(terminal) racemes	fewer flowers on the average	more flowers on the average
rosette-like lateral shoots	normally present	normally absent
flowers and most floral parts	larger on the average	smaller on the average
sepals	always longer than 4 mm	nearly always smaller than 4 mm
anthers	2.0–2.7 mm long	1–2.0 mm long
flowering time	as a whole later	as a whole earlier

ECOLOGY

Decaploids usually occurred in situations where the roots reach the (ground-) water always or for the greater part of the year. Once a population with $2n = c.70$ was found in a streamlet 40–50 cm below the water level (Heelsum).

Tetraploids were usually met with in dryer habitats. Their roots seldom reach the (ground-)water. They showed a rather great amplitude with regard to the water content of the soil. Although octoploids have been found in the same places as tetraploids, they usually prefer wetter habitats.

These records confirm those of BANACH (1951) and LÖVKVIST (1956).

TAXONOMY

The results obtained from this study demonstrate the presence of two groups of individuals in *C. pratensis* L. in the Netherlands. These groups are cytologically separable, nearly always morphologically distinguishable, and ecologically different, restrictions in compatibility are more or less evident. This is a confirmation of the results of LÖVKVIST (1956).

Instead of assigning specific status to the groups, the author prefers to treat them as subspecies, namely octoploids and decaploids as *C. pratensis* L. ssp. *palustris* (Wimm. and Grab.) Janch., and tetraploids as *C. pratensis* L. ssp. *pratensis*.

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ELECTRON MICROSCOPIC STRUCTURE OF THE ALEURON CELLS OF BARLEY DURING GERMINATION

A. A. VAN DER EB[1]) AND P. J. NIEUWDORP

(*Laboratory of General and Technical Biology, Technological University, Delft, The Netherlands*)

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ABSTRACT

Germinating barley aleuron cells were studied electron-microscopically.

The *aleuron grains*, after $KMnO_4$-fixation and embedding in Vestopal W, contain a protein matrix, electron-dense, and electron-transparent bodies. Evidence is presented that the electron-dense bodies are globoids which consist of phytin. The nature of the electron-transparent bodies is discussed. During germination the protein matrix disappears and the globoids are decomposed.

The *rough-surfaced er* develops extensively in the first 8 days. It forms protein vesicles which seem to discharge their contents in the vicinity of the cell wall. The latter appears to be subject to chemical change. In the course of the process of germination the er makes connections with the spherosomes.

The *spherosomes* are for the greater part found around the aleuron grains. During germination their contents gradually diminish.

In the first 8 days the *mitochondria*, very undeveloped at the start, obtain more and longer cristae.

The cytological changes observed reflect the known physiological activities of the aleuron cells.

INTRODUCTION

The cells of the outer layers of the cereal endosperm contain a great number of large aleuron grains. They are called aleuron cells. In *Hordeum*, the aleuron layer, which is approximately three cell layers thick at the convex side of the seed, completely envelops the endosperm except where it is adjacent to the embryo. Besides protein, the aleuron layer contains fat; starch is absent. During germination the cell walls and the starch of the endosperm are broken down and used by the developing embryo. This process starts in the vicinity of the scutellum and proceeds in an apical direction along the aleuron layer (BROWN and ESCOMBE, 1898) since the necessary enzymes are produced and secreted by both these tissues.

In recent years much research has been done on the production of enzymes by the aleuron layer (YOMO, 1958, 1960; YOMO and INUMA, 1962, 1963, 1964; PALEG, 1960a, b, 1961; PALEG, SPARROW and JENNINGS, 1962; PALEG, COOMBE and BUTTROSE, 1962; MACLEOD and MILLAR, 1962; BRIGGS, 1963, 1964; VARNER, 1964; LAZER, BAUMGARTNER and DAHLSTROM, 1961). It was established that a

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1) The junior author, at present Mrs. A. A. van der Linden-van der Eb, has made this study in partial fulfilment of the requirement for her Master's degree.

gibberellic hormone stimulates the production of enzymes by the aleuron layer. This hormone is secreted by the embryo (YOMO, 1960) and penetrates the endosperm through the scutellum. The enzymes must be synthesized *de novo*, since they were found to be heavily labeled if labeled amino acids had been supplied at an early stage (VARNER, 1964). Accordingly, respiration appears to be indispensable for enzyme synthesis (MACLEOD and MILLAR, 1962; VARNER, 1964).

The changes in the structure of the protoplasm which accompany the production of enzymes by gibberellic acid-treated aleuron cells have been studied to some extent with the aid of the electron microscope. These cells contain aleuron grains – which are large vacuoles filled with reserve-protein (DANGEARD, 1922; BUVAT, 1962; POUX, 1962) – and lipid droplets called spherosomes. The aleuron grains are supposed to have originated from dilations of the endoplasmic reticulum (POUX, 1962; BUTTROSE, 1963a, b). They are not homogeneous since they may contain one or more electron-dense as well as some electron-transparent globules (HYDE and PALEG, 1963). So far, the character of these structures is not quite clear. Possibly owing to the use of acid media for fixing and rinsing (see Discussion), POUX (1963) observed no electron-dense, but only more or less electron-transparent globules in the aleuron grains of wheat aleuron cells. Since she could demonstrate that acid phosphatase was localized especially at the inner surface of the delimiting membrane of the globules, she concluded that the latter might be phytin-containing globoids.

HYDE and PALEG (1963) and PALEG and HYDE (1964) observed both electron-dense and electron-transparent round bodies in the aleuron grains of barley aleuron cells, after $KMnO_4$-fixation as well as after OsO_4-fixation. The bodies which were electron-dense after $KMnO_4$-fixation were electron-transparent after OsO_4-fixation and would contain protein, while the spheres which were electron-transparent after $KMnO_4$-fixation were dense after OsO_4-fixation and would contain lipid.

MACLEOD, JOHNSTON and DUFFUS (1964) call the $KMnO_4$-fixed electron-transparent bodies in their material vacuoles, and the dense ones, inclusion bodies.

So far, no changes in the ultrastructure have been reported that might be more directly related to the extensive *de novo* enzyme synthesis. Therefore, we studied this point in particular. Further, we tried to elucidate the character of the electron-dense and the electron-transparent spheres in the aleuron grains.

METHODS

The methods and materials used were primarily those of NIEUWDORP and BUYS (1964). Grains of *Hordeum vulgare* cultivar 'Proctor' were germinated at 11° C. Nearly all specimens were fixed with $KMnO_4$, which gave the best results, and were embedded in Vestopal W.

We always attempted to obtain sections from an area several cells above the apical end of the scutellum (Figs. 1 and 2). This is rather important since the greater the distance from the scutellum, the later the cell will be triggered into activity by the scutellum hormone. However, we were not always successful in this respect, and thus we sometimes found a younger stage than expected with regard to the number of days germination had lasted.

We found but little difference in ultrastructure between the outer and the inner cells of the same radial row of aleuron cells. Therefore, later on we did not try to localize the cells in this respect.

RESULTS: THE ELECTRON MICROGRAPHS

Figure 3. The protoplasm in the resting stage. Spherosomes (s) and aleuron grains (a) are conspicuous, but no endoplasmic reticulum is apparent. The spherosomes are so electron-transparent that they may be considered empty. Their sole contents may have been lipid which was dissolved in the acetone used for dehydration of the specimen. The majority of the spherosomes are part of a single layer surrounding each aleuron grain. The aleuron grains contain globular bodies of two kinds, which appear in the micrographs as black (electron-dense) and white (electron-transparent) circular areas. The black ones often show irregularities due to sectioning, which suggests hardness. The white areas have a distinct black envelope.

Figure 4. The protoplasm of an aleuron cell of a seed germinated for 5 days. Some plasma membranes and some mitochondria (m) with inconspicuous cristae are visible. The dark envelope of the electron-transparent circular area in the aleuron grain now has a greyish, granular inner margin. The spherosome membranes have slightly shrivelled and their content has an irregular light-greyish hue.

Figure 5. The protoplasm after 6 days germination. The section has been contrasted with Pb, to which the wide, grey border within the spherosomes is evidently due. The electron-transparent globules in the aleuron grain have expanded at the expense of the protein matrix. Their outlines are now often undulated and they contain some granular material partly arranged in circles.

Figure 6. After 8 days germination. The electron-transparent globules in the aleuron grains have further dilated. The electron-dense body now shows an indistinct outline, and electron-dense material is scattered in the protein matrix. The spherosome membranes have shrivelled still more and their contents are now denser. In this electron micrograph the endoplasmic reticulum (er), with local swellings, is distinctly visible. The mitochondria (m) have more cristae and are outlined more sharply. Small globular bodies – probably protein vesicles – appear in the cytoplasm (pr).

Figure 7. Part of a cell of a seed which was also germinated for 8 days. This cell has passed through further changes. The upper half of the micrograph shows part of a nucleus (n) with nuclear envelope (ne) with pores (np). In the lower part is a comparatively

small aleuron grain, the contents of which have almost completely dissolved. It is still surrounded by spherosomes (s) which are transparent as usual after $KMnO_4$-fixation if the section has not been contrasted with Pb. A few spherosomes in the vicinity of the nucleus have reached a more advanced stage of development as appears from their contents being more electron-dense.

The endoplasmic reticulum (er) is strongly developed, forming stacks of parallel lamellae. In the vicinity of the aleuron grain the ends of the er are club-shaped. The contents are more electron-dense than the surrounding cytoplasm. This also applies to the contents of the 'protein vesicles' (pr) which may be transverse or oblique sections through swollen er.

Figure 8. Also after 8 days germination. The protoplasm near the cell wall (w). 'Protein vesicles' are present both in the vicinity of the cell wall and farther away from it. The cell wall is now electron-dense, whereas it is always transparent in samples germinated for only a few days. This is indicative of a profound change in the chemical composition of the cell wall.

Figure 9. Also after 8 days germination. The upper part of the micrograph shows an aleuron grain, most of the protein of which has dissolved. In the lower part a leucoplast (l), spherosomes and endoplasmic reticulum, the latter with electron-dense swellings. In between, are many vesicles with contents of similar density. Nearly all of the spherosomes in this micrograph are somewhat electron-dense though the section was not treated with Pb acetate.

Figure 10. After 10 days germination. The cell wall is severely attacked. In the adjacent cytoplasm many vesicles and tubules of the er occur, several of which seem to discharge their contents into the wall. Note the intercellular connection (ic) in the cell wall.

Figure 11. Also after 10 days germination. In the right-hand upper corner a portion of a cell wall with indistinct plasmalemma and in the right-hand lower corner an aleuron grain are visible. The spherosome membranes have shrivelled further. Protuberances of the spherosomes seem to trail into appendages connected with the endoplasmic reticulum (arrow). There are too many 'protein vesicles' to consider them all transverse or oblique sections through swellings of the endoplasmic reticulum (see p. 696).

Figure 12. Also after 10 days germination. A small aleuron grain is nearly filled by an apparently disintegrating electron-dense body. Spherosomes connected with the er through protuberances, and mitochondria are present.

Figure 13. From the same stage as Figs. 10–12, shows an obvious connection between the er and a spherosome (arrow).

Figure 14. After 17 days germination. The upper half of the micrograph shows an aleuron grain enclosing an undissolved electron-dense body (gl). To the left in the lower half is a completely dissolved aleuron grain (a) surrounded by small, very electron-dense spherosomes. The protein vesicles (pr) have increased in size. Active mitochondria are still present.

Figure 15. After 7 days germination. This specimen was OsO_4-fixed in order to show both the free ribosomes (ri) and those adhering to the er, which thus form the rough surface of the er. After OsO_4-fixation the contents of the spherosomes are not dissolved (cf. Fig. 3).

Figure 16. Part of an aleuron cell of a full-grown barley seed, 35 days after flowering. The seed was still ripening and beginning to yellow. Spherosomes are numerous. The developing aleuron grains consist only of a small vacuole which is nearly completely filled by an electron-dense globule.

Figure 17. After 8 days germination. This specimen was fixed with 5% glutaraldehyde, left overnight at 0° C, thoroughly rinsed and then treated with OsO_4. The electron density of the dense globules has increased so much that the electron beam caused heat deformations (boiling bubbles). The less dense sphere in the aleuron grain, which after $KMnO_4$-fixation is usually transparent, now is somewhat more dense than the protein matrix.

Figure 18. After 7 days germination. The specimen was fixed with glutaraldehyde only. Even so, the bodies which are electron-dense after fixation with $KMnO_4$ or OsO_4 are of a dark shade. This proves that their electron density is not entirely due to $KMnO_4$ or OsO_4. Besides the aleuron grains, spherosomes are faintly visible.

INTERPRETATION OF THE MICROGRAPHS AND DISCUSSION

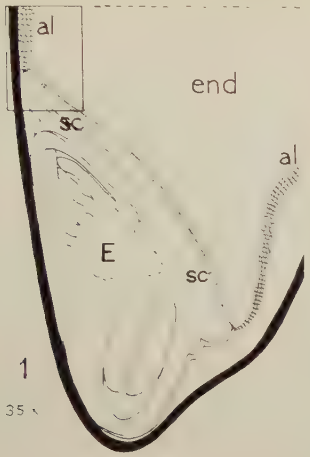
The changes in the structure of the diverse organelles during germination will now be discussed.

Aleuron grains

The aleuron vacuoles in the maturing barley seed are smaller than they will be in the mature seed. Each vacuole is for the greater part filled by an electron-dense globule, the globoid.

In the mature barley seed protein is the major component of the aleuron vacuoles, or aleuron grains, both in aleuron cells (Fig. 3) and in scutellum epidermis cells (NIEUWDORP, 1963). The aleuron grains contain a protein matrix enclosing, among other things, one or more electron-transparent, and one or more electron-dense globules. The former were called 'internal cavities' by NIEUWDORP (1963) and NIEUWDORP and BUYS (1964). In dry seeds, they would be air-filled; in soaked seeds, they would be filled with an aqueous solution. They were assumed to have been formed during maturation by a process of precipitation of the protein from the liquid in the vacuole. During germination this process would be reversed, the internal cavities enlarging at the expense of the protein matrix which dissolves in the aqueous solution in the course of ca. 8 days (Fig. 7). During fixation of the specimen with $KMnO_4$ the dissolved protein probably precipitates in different forms (Figs. 4–7). After fixation with glutaraldehyde followed by OsO_4, however, the contents of the internal cavities seem to be homogeneous (Fig. 17).

A. A. VAN DER EB AND P. J. NIEUWDORP: *Electron microscopic structure of the aleuron cells of barley during germination.*



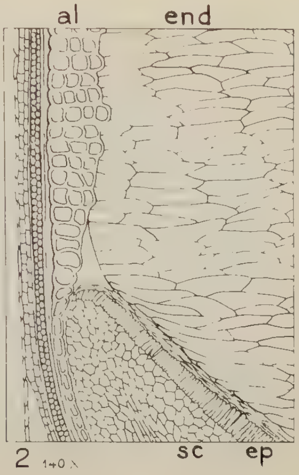


Fig. 1. Part of a longitudinal section of a barley seed.

Fig. 2. Part of Fig. 1 enlarged, to show the site of the ultra-thin sections.

PLATE I

ABBREVIATIONS TO FIGS. 3–18

a	aleuron grain (protein vacuole)
al	aleuron layer
E	embryo
end	endosperm
ep	epithelium
er	endoplasmic reticulum
gl	globoid
ic	intercellular connection (plasmodesma)
l	leucoplast
m	mitochondrion
n	nucleus
ne	nuclear envelope
np	nuclear envelope pore
pr	protein vesicle
ri	ribosome
s	spherosome
sc	scutellum
w	cell wall

Facing p. 694

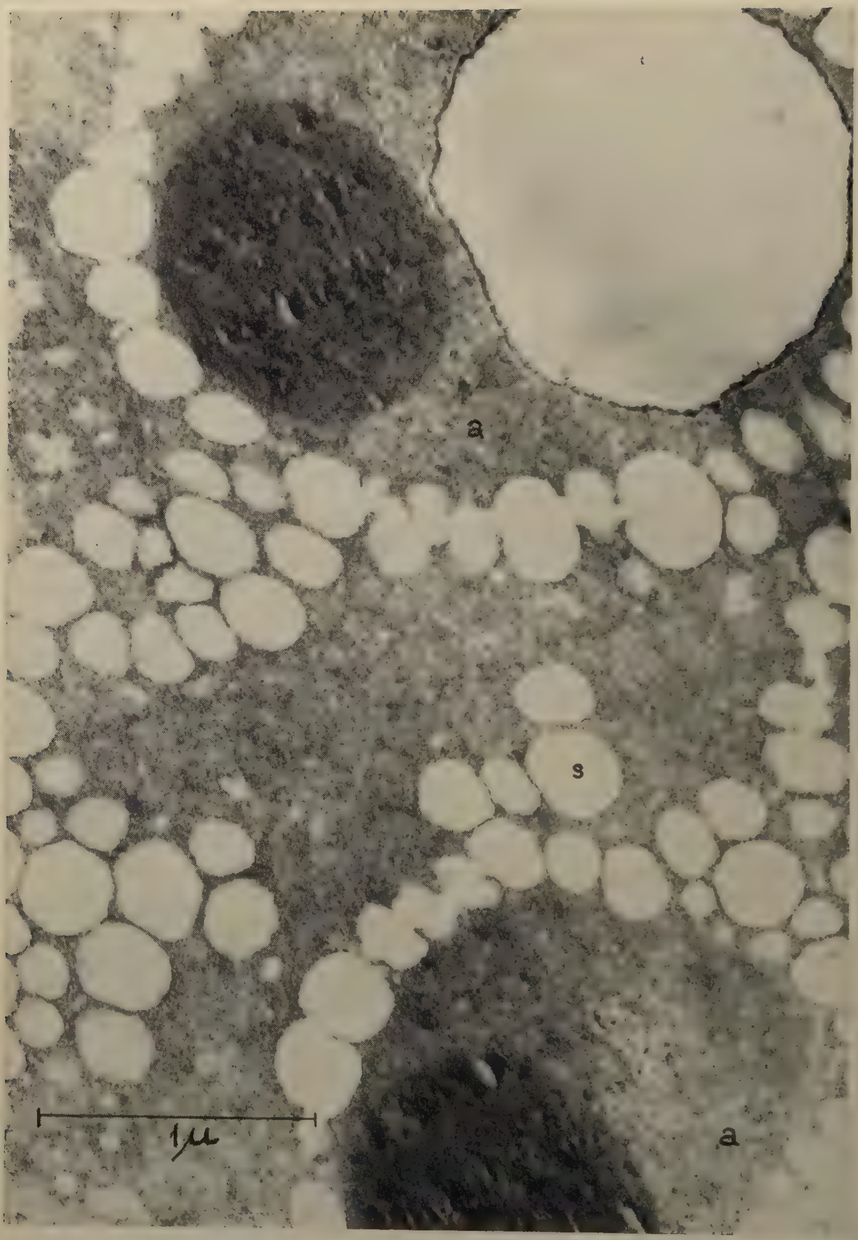


Fig. 3. Part of the protoplast of an aleuron cell in a barley seed soaked in water for 24 h at 0° C. $KMnO_4$-fixation.

PLATE II

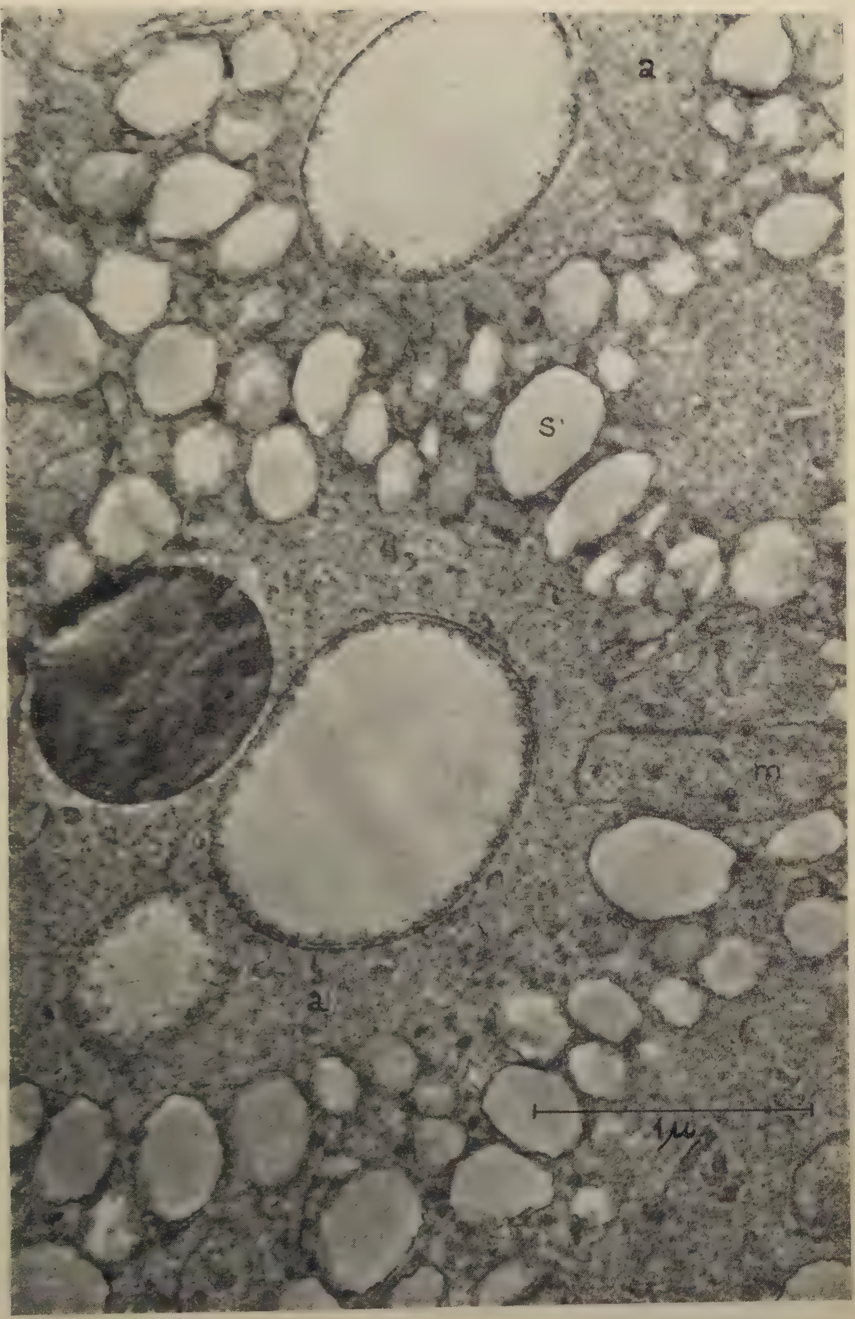


Fig. 4. Part of the protoplast after 5 days germination at 11° C. $KMnO_4$-fixation.

PLATE III

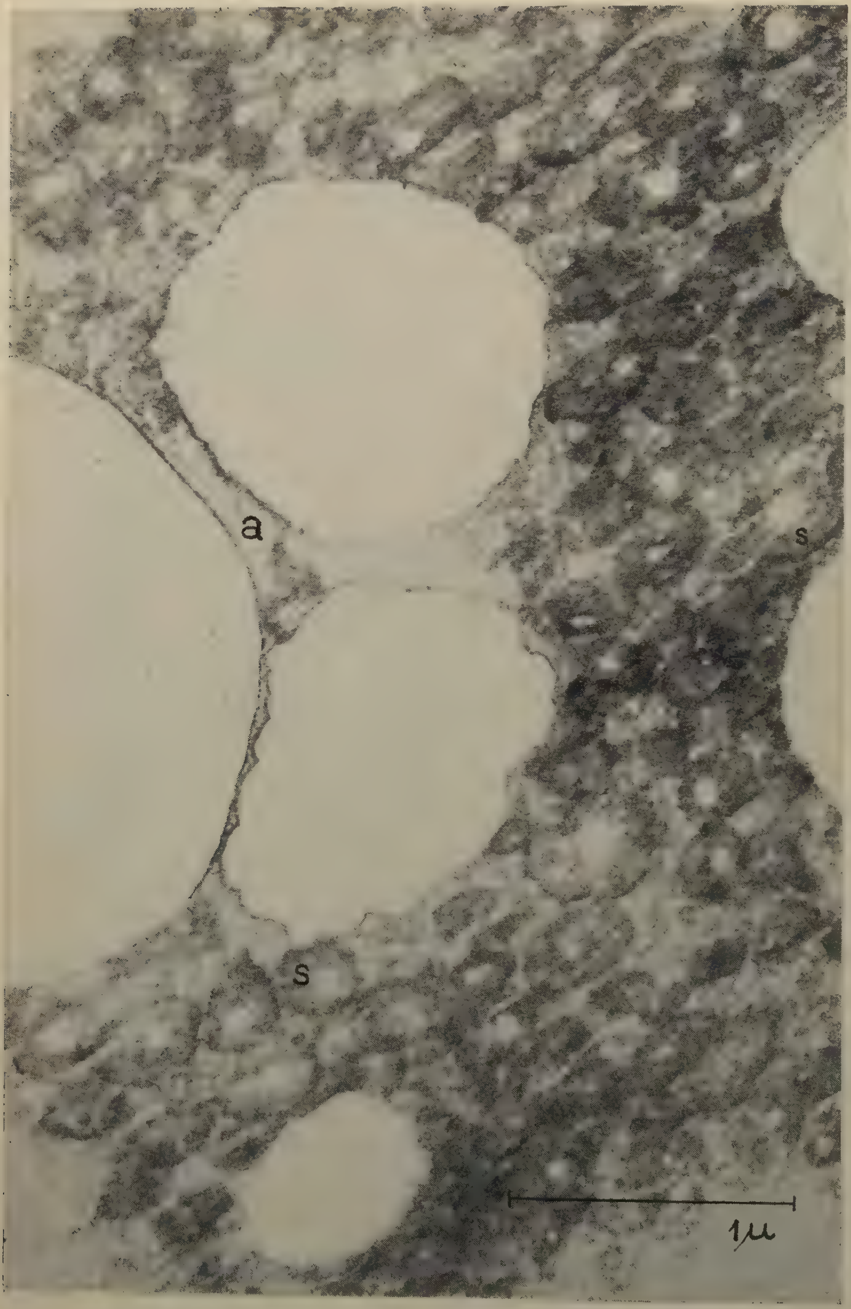


Fig. 5. After 6 days germination. $KMnO_4$-fixed and section contrasted with Pb.

PLATE IV

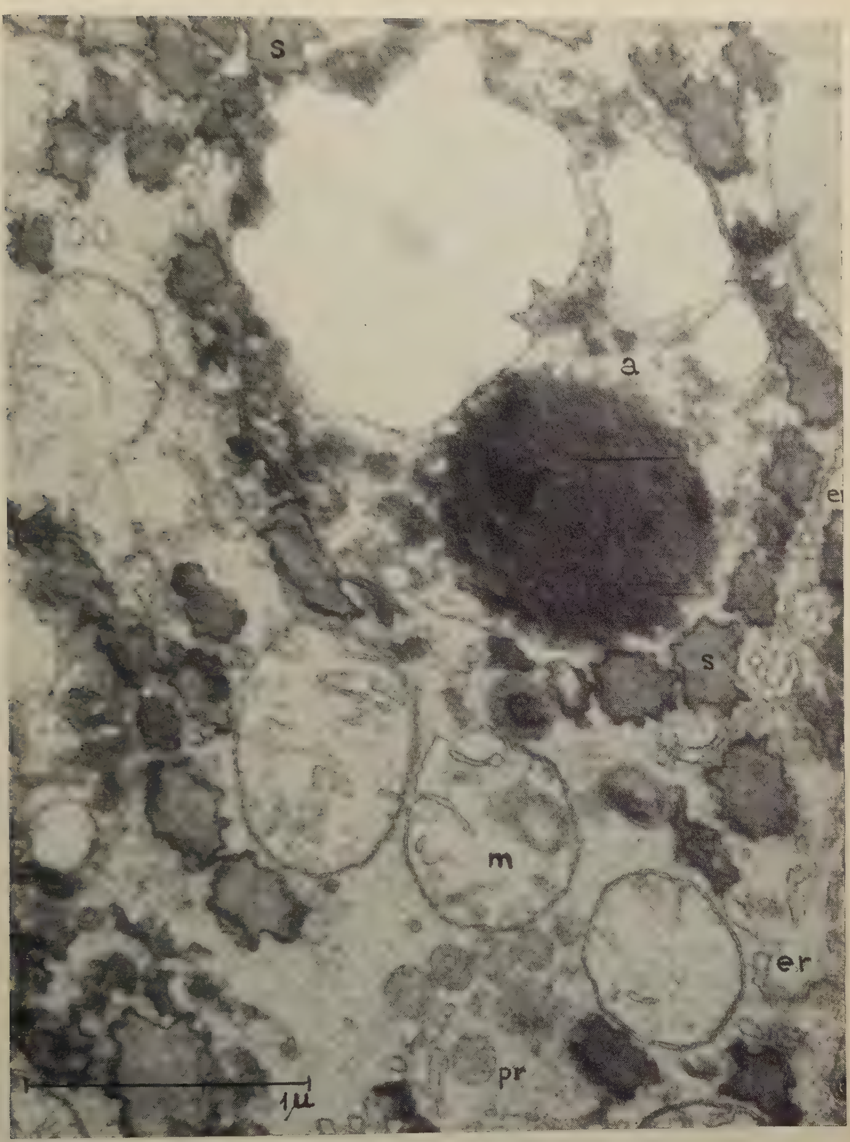


Fig. 6. After 8 days germination. $KMnO_4$-fixed and section contrasted with Pb.

PLATE V

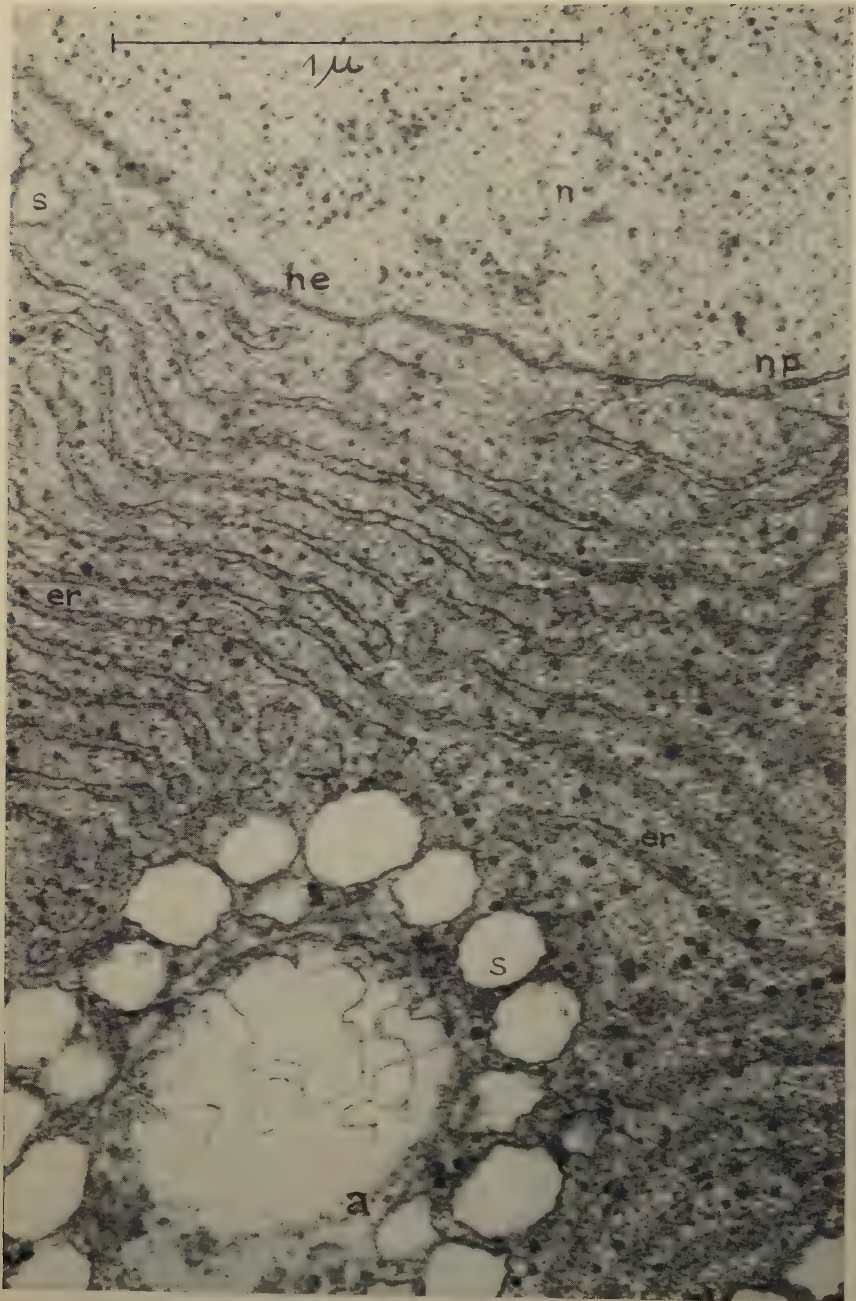


Fig. 7. After 8 days germination. $KMnO_4$-fixed.

PLATE VI

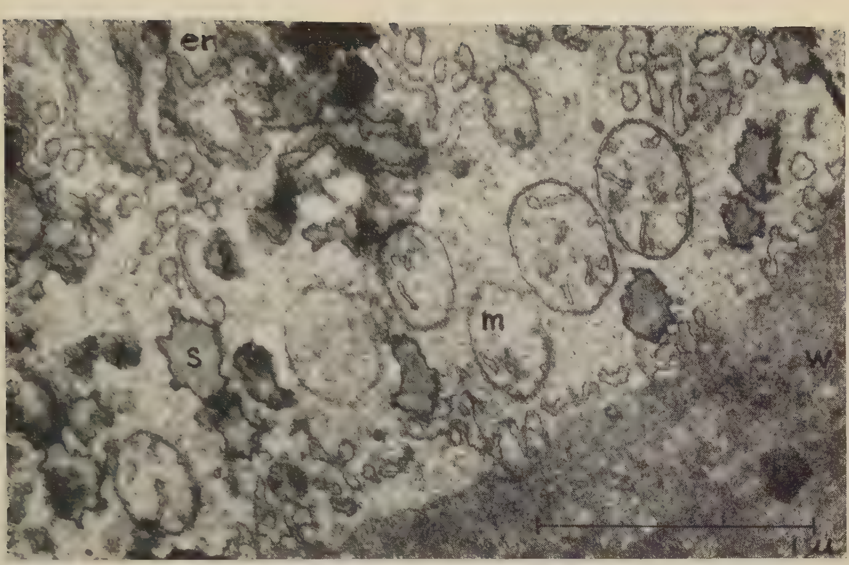


Fig. 8. After 8 days germination. Protoplast and cell wall. $KMnO_4$-fixed and section contrasted with Pb.

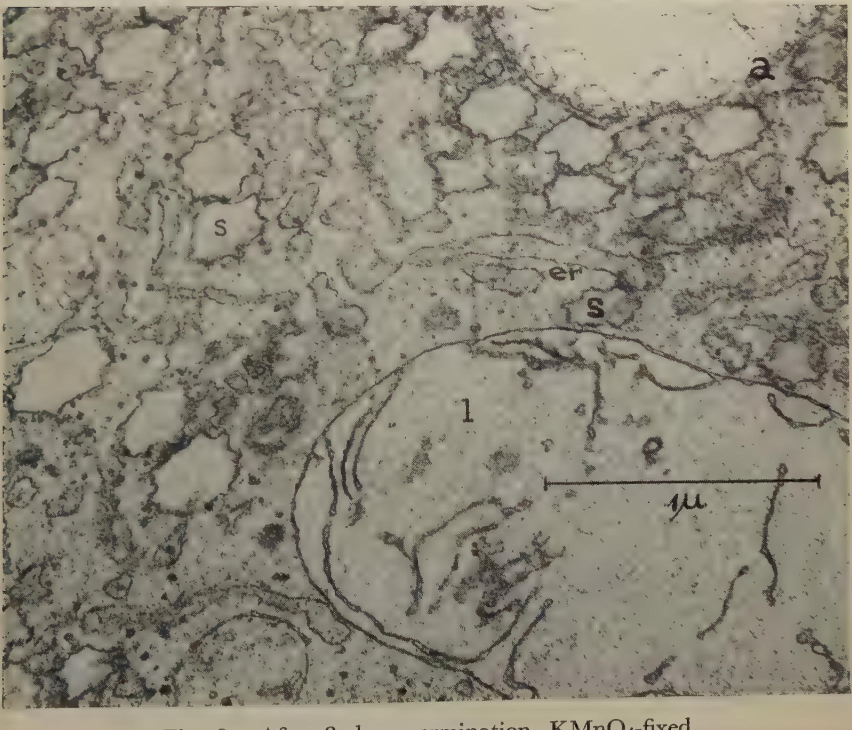


Fig. 9. After 8 days germination. $KMnO_4$-fixed.

PLATE VII

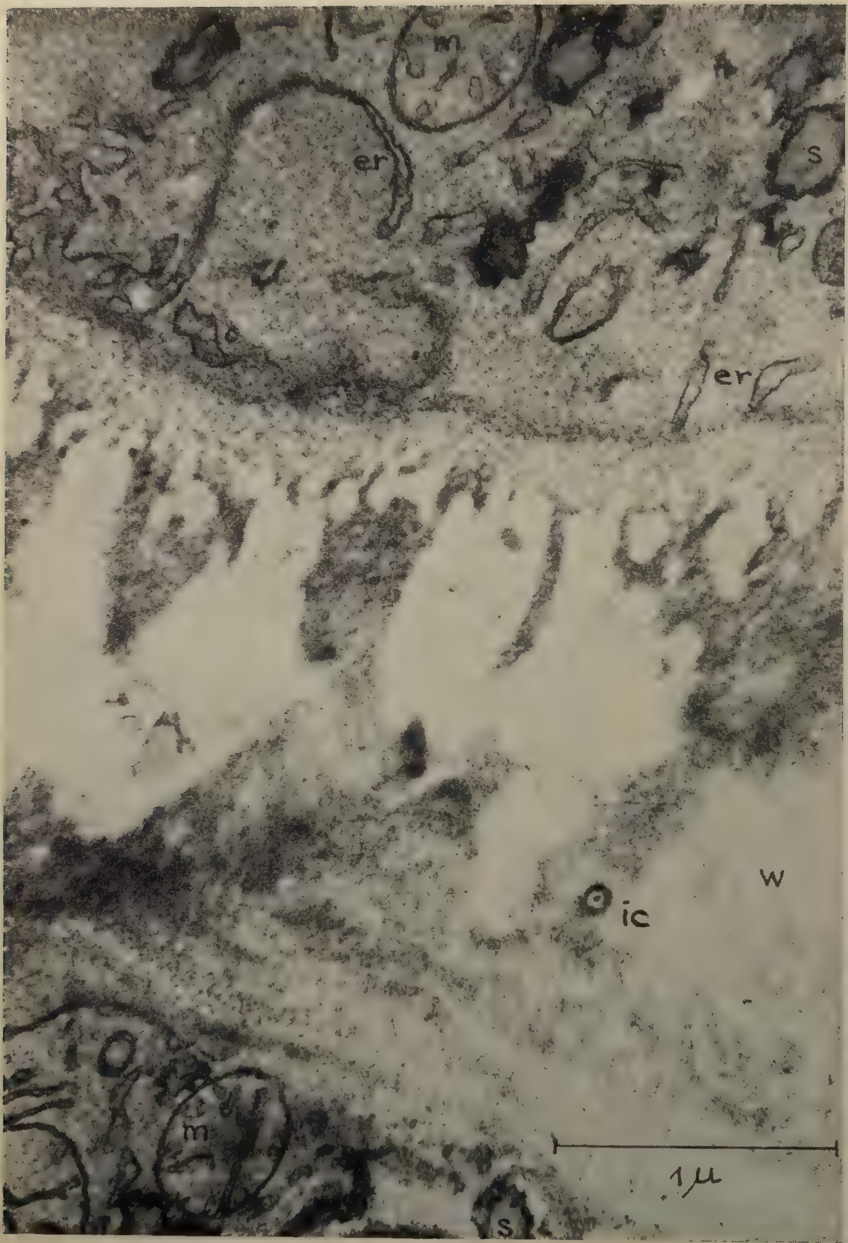


Fig. 10. After 10 days germination. Cell wall and adjacent protoplasm. $KMnO_4$-fixed.

PLATE VIII

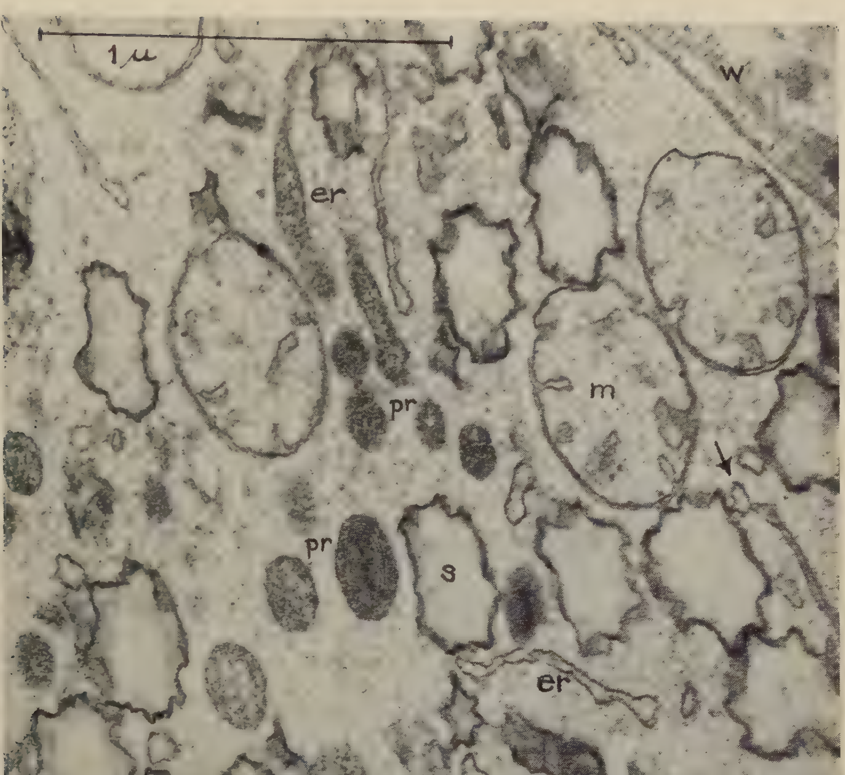
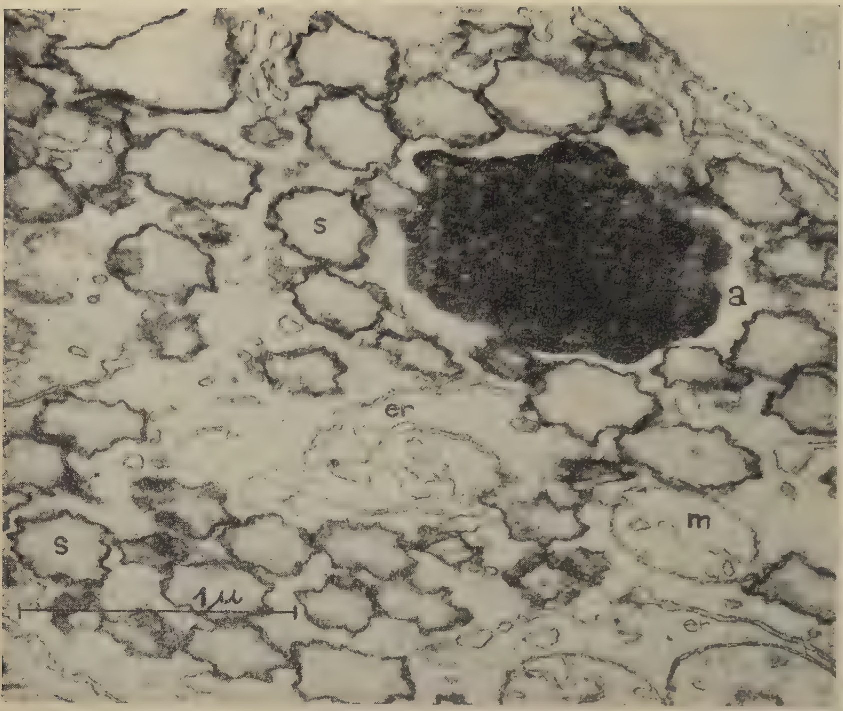
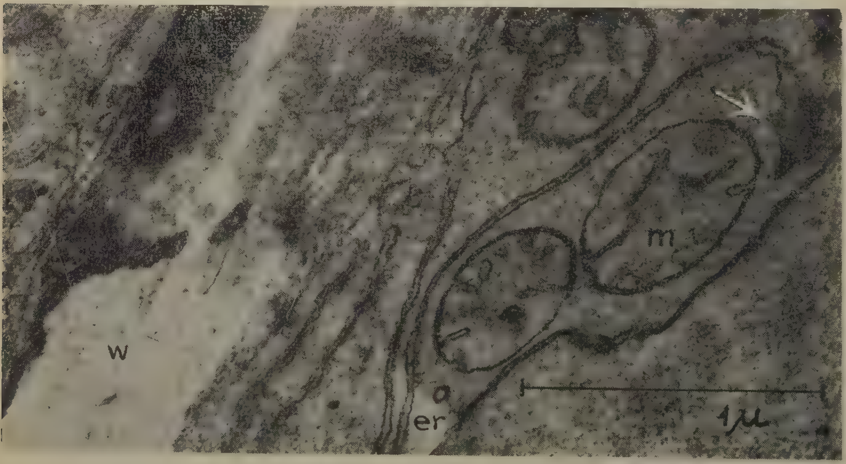


Fig. 11. After 10 days germination. $KMnO_4$-fixed.

PLATE IX





Figs. 12 and 13. After 10 days germination. $KMnO_4$-fixed.

PLATE X

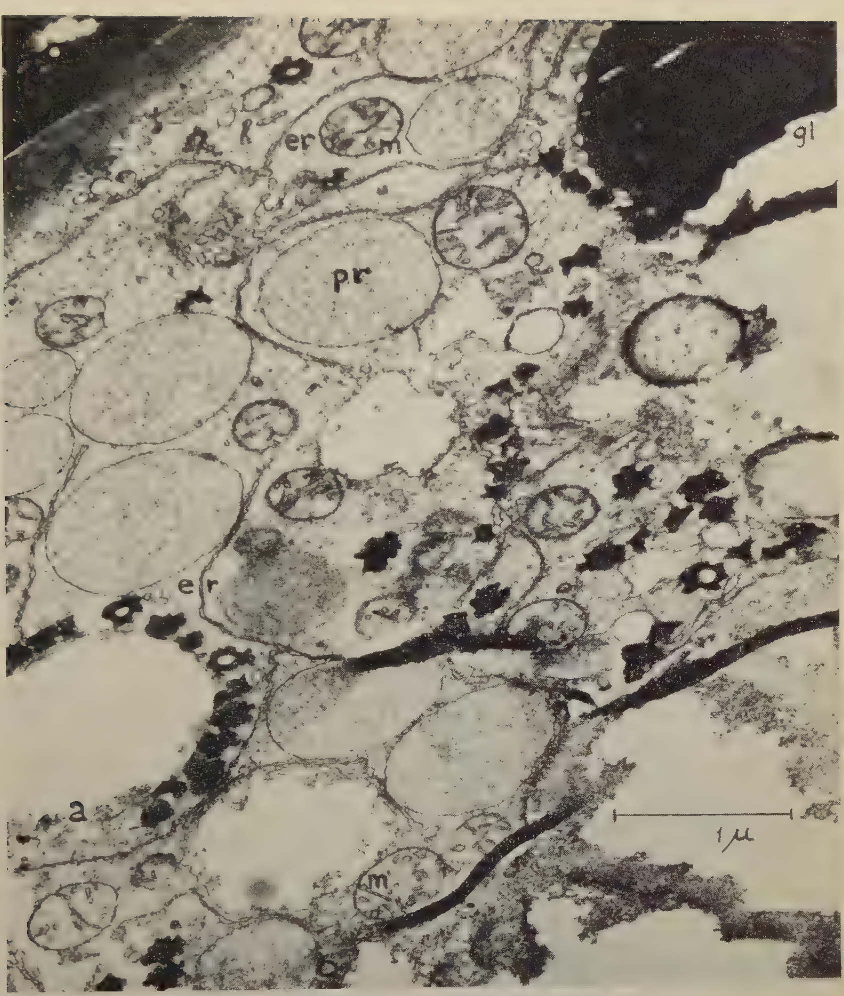


Fig. 14. After 17 days germination. $KMnO_4$-fixed and section contrasted with Pb.

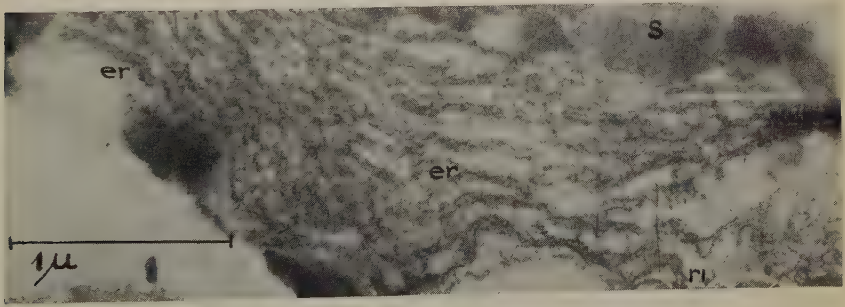


Fig. 15. After 7 days germination. OsO_4-fixed.

PLATE XI

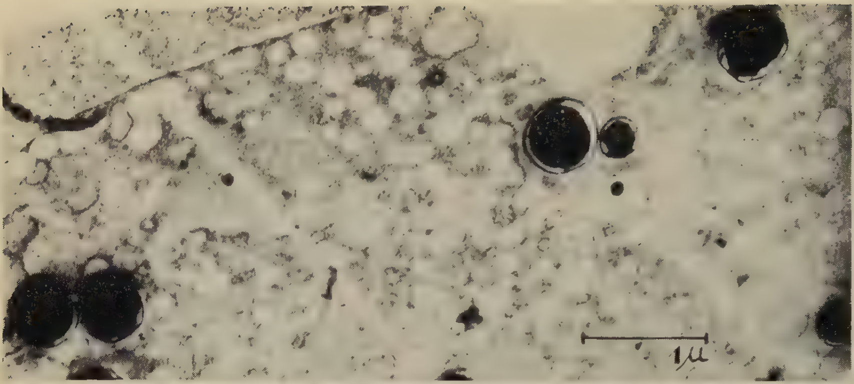


Fig. 16. Thirty-five days after anthesis. $KMnO_4$-fixed.

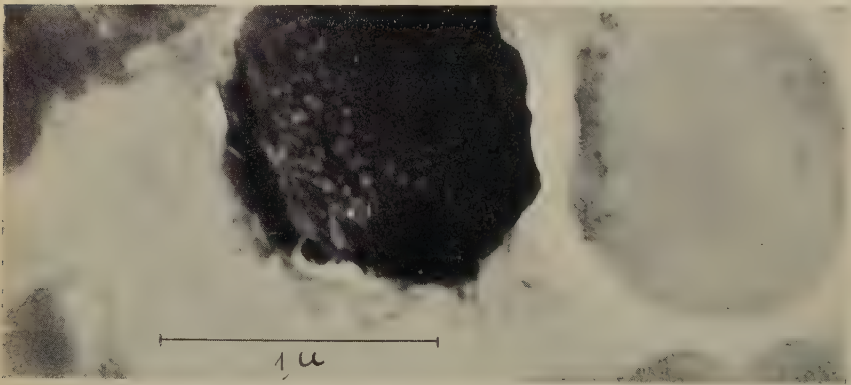


Fig. 17. After 8 days germination. Fixed with glutaraldehyde followed by OsO_4.

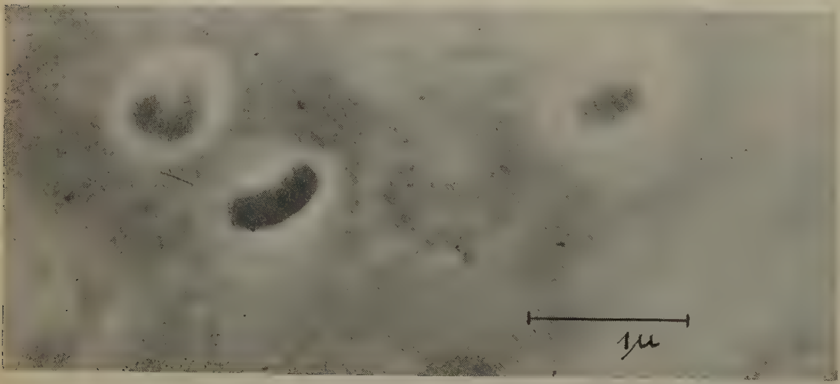


Fig. 18. After 7 days germination. Fixed with glutaraldehyde.

PLATE XII

Since Poux (1963) found acid phosphatase in aleuron grains one might suppose that the aleuron protein would consist mainly of enzymes which would merely need be dissolved and transported to the starchy part of the endosperm. However, since *de novo* synthesis, i.e. from amino acids, of at least α-amylase has been demonstrated (Varner, 1964; Briggs, 1964) it seems more likely that the aleuron protein is a true reserve protein which is hydrolyzed into amino acids, the latter being the building units for the enzymes.

Aleuron grains in aleuron cells always contain one or more electron-dense globules (Figs. 3, 4, 6, 16) which we consider to be identical with the light-microscopically observed globoids. These are known to consist mainly of phytin (Ca-Mg-inositol-hexaphosphate). Phytin, due to the elements Ca, Mg and P, may be expected to scatter electrons heavily. As a model experiment, we dried very small droplets of a phytin solution on a formvar membrane. In the electron microscope they were so electron-dense that they 'boiled'. In harmony with this result it was found that the globoids were electron-dense even when the specimen had been fixed only with glutaraldehyde. Subsequent treatment of the specimen with OsO_4 made the globoid so dense, that the boiling effect was observed (Fig. 17). This concept is also supported by the considerable hardness indicated by the unevenness of the sectioned globoids (Fig. 3). Poux (1963a, b), on the other hand, found electron-transparent globoids in embryonic wheat tissue, but this result may be explained by the fact that she used acid solutions for fixing and rinsing in order to be able to demonstrate acid phosphatase. These acid solutions may have dissolved and extracted the phytin. In a recent article Poux (1965) mentioned a same procedure applied to the seeds of *Linum* and *Cucumis*. In both these species the aleuron grains were found to contain crystalloids. The observations of Paleg and Hyde (1964) are consistent with our concept (though their conclusions are different from ours), and it is also supported by the finding of globoids in green malt (Vazart, 1960).

During germination the globoids are attacked, although much slower than the protein matrix. After ca. 8 days their outlines become irregular, some material lying scattered in the protein matrix (Fig. 6). Even after 17 days a major part of the original globoid is still found in the aleuron grains which by that time are devoid of protein (Fig. 14).

A similar phenomenon was observed in aleuron grains of scutellum epidermis cells where globoid-like bodies remained intact for a long time (Nieuwdorp and Buys, 1964). In the corresponding cells of non-germinated barley, however, Nieuwdorp (1963) did not find globoids in the aleuron grains.

Aleuron grains are known to originate from endoplasmic reticulum. In scutellum epidermis cells we incidentally found a few connections, but unlike Paleg and Hyde (1964) we did not find any in aleuron cells. We assume that the connections observed by these authors were due to the treatment of the seeds, viz. soaking at 30° C for 1–2 days and subsequent separation of the aleuron layer from the starchy endosperm.

Endoplasmic reticulum (*er*)

Whereas in scutellum epidermis cells of barley seeds soaked in water for one day at 0° C some endoplasmic reticulum was found (NIEUWDORP, 1963) which rapidly increased during germination until it reached a peak within seven days (NIEUWDORP and BUYS, 1964), we did not find any er in resting aleuron cells. After 5 days germination some er appeared (Fig. 4) which further increased until the 8th day (Fig. 7). Thus the development of the er in the aleuron cells lags behind that of the er in scutellum epidermis cells. This may be due to one or more of the following factors: a) the absence of er in resting aleuron cells as compared to the presence of a small amount in scutellum epidermis cells, b) the need for stimulation, directly or indirectly, by gibberellin or some other hormone, and c) a difference in the rate of imbibition of the aleuron cells and the scutellum epidermis cells during the soaking of the seed.

When fully developed, the er in the aleuron cells forms stacks of parallel rough-surfaced lamellae, a structure typical for plant and animal cells which produce and secrete large quantities of proteins. Such structures are lacking in scutellum cells. Besides, free ribosomes occur (Fig. 15).

After the development of the er has reached its peak a decline already visible after ca. 2 days sets in (Figs. 10–13). At this stage, and later, the er shows many local swellings filled with relatively electron-dense material. At first, the swellings are formed mainly in the vicinity of aleuron grains (Fig. 7); later on they are formed in all parts of the er. Some enlarge and disconnect themselves, thus becoming what we called protein vesicles with a diameter of 0.125–0.2 μ (Fig. 11). The vesicles usually have granular contents indicative of protein; in some of them concentric structures occur. Since many such vesicles were found near cell walls which at the same time had become unusually electron-dense, it can be inferred that the vesicles discharge their contents into the walls which they must pass on their way to the starchy part of the endosperm. Burst vesicles are seen near the wall (Fig. 10). This suggests decomposition of the wall by the hypothetical enzymes of the vesicles (Figs. 8, 10). Protein vesicles were found up to the end of the germination process; in the latest stage many were considerably larger (Fig. 14).

In developing endosperm of wheat grains BUTTROSE (1963a, b) described protein vesicles containing protein bodies. In larger vacuoles GRAHAM *et al.* (1962) and JENNINGS *et al.* (1963) observed several protein bodies which had supposedly been secreted by the er; thus, there is a process of secretion within the endosperm cell. JENNINGS *et al.* (1963) described the occurrence of multi-layered sheets between protein bodies and vacuolar membranes. We have never observed similar structures in the aleuron cells of germinating barley, except in one body with concentric layers (Fig. 11).

The vesicles we found in aleuron cells did not occur in scutellum epidermis cells, but dilations of the er were found also in the latter tissue. In scutellum epidermis cells, on the other hand, much smaller vesicles, probably derived from the Golgi apparatus did occur (NIEUWDORP, 1963; NIEUWDORP and BUYS, 1964). Neither the Golgi apparatus, nor the latter kind of vesicles were often found in aleuron cells.

Connections between the er and aleuron grains were never observed.

Spherosomes

In resting seeds and in those germinated for less than 5 days, the spherosomes are spherical vesicles of ca. 0.4 μ in diameter, with smooth surfaces; most of them are found surrounding aleuron grains. In $KMnO_4$-fixed specimens their contents have disappeared, probably because the lipid material has been dissolved in the acetone used in the embedding procedure.

In more advanced stages of germination the spherosomes were found to have altered in several respects. Firstly, the peripheral parts have become less soluble in acetone and showed up after $KMnO_4$-fixation (Figs. 10, 11) and more conspicuously after subsequent contrasting with Pb (Figs. 5, 6, 8). The change may be due to the formation of fatty acids as a result of lipolysis. Secondly, after 5 or more days of germination the smooth outline has become irregular, indicating a surface of troughs and ridges. This may be due to surface growth of the envelope without corresponding growth in volume, but a decrease in volume without diminution of membrane surface is more probable since the change in appearance coincides with the chemical change mentioned and since in still later stages many spherosomes have disappeared while the remaining ones have obviously decreased in size (Fig. 14). This is in accordance with the fact that after 10 or more days of germination connections have formed between the er and the spherosomes (Figs. 11–13). Their contents are likely to have dissolved. Still, a small number of spherosomes persist even after 19 days germination.

Mitochondria

In cells of the resting seed the mitochondria have few cristea and the latter are poorly developed. During germination the cristae increase in number and in size and their membranes become more electron-dense. This becomes visible after 8 days, whereas in scutellum epidermis cells the same stage is already reached after 3 days. Also the enveloping membranes of the mitochondria become more electron-dense. Double membranes are now clearly visible, but for considerable parts the outer membrane is lacking which makes the cristae look like open-mouthed tubules (Figs. 6, 8, 11, 13, 14). Is this an indication of increased metabolism? This would be in line with the observation of VARNER (1964) that respiration is essential for amylase synthesis. The mitochondria persist after 19 days germination (Fig. 14).

TABLE 1

Changes in the aleuron cells of germinating barley *as observed after* KMnO$_4$-*fixation*

	0 days	5–6 days	6–8 days	10 days	17–19 c
Cell wall	light; fibrillar	irregularly darkening (due to change in chemical compostion)			dark-gr fibrillar
Er	not found	visible	increased in size; local dilations; contact with, and release of material to cell wall; contact with spherosomes		decrease
Spherosomes	electron-transparent; contents dissolved; spheres	greyish border; irregular spheres	dark; forming appendages	contact with er	decrease in numl
Mitochondria	not found	becoming visible	clearly visible; increased cristae		reduced
Aleuron grain					
matrix	dark	more transparent		dissolved	
globoid	black		some dissolved		reduced
transparent cavity	clear	borders become granular; outlines undulated			vanished

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Dr. Ir. L. Bos, Virussen en planten, 1965, 277 pp. Edited by W. E. J. Tjeenk Willink, Zwolle, Netherlands. F. 32.50.

This book intends to be an introduction for those students who wish to become acquainted with the principles of plant virology. After a short history of the study of virus diseases the first part of the book is dedicated to methods of inoculation, the appearance of symptoms and their variable character, virus transmission and epidemiology including economic importance of virus diseases. In the second part methods of virus isolation and purification are described as well as methods in use for diagnostic purposes such as serology and electron microscopy. How to define the identity of a virus and the problems encountered in virus nomenclature are briefly though clearly discussed.

The last part of the book deals with practical problems: how to control virus diseases by spraying, by hygienic measurements or hot water treatment, how to eliminate diseased plant material by laboratory tests or to improve the resistance by breeding. It is not surprising that this part of the book gives a good deal of information on potato virus diseases and on the Dutch organisations in charge of crop protection and disease control. A limited number of standard publications and general papers are mentioned at the end of each chapter. Finally a list of the most important handbooks is added.

The subjects dealt with are well chosen from the big field of virology. On purpose the author discusses only occasionally questionable problems and therefore the reader will generally agree with his information that is well defined. Moreover many carefully gathered illustrations are added. It is clear that the text was originally meant for instruction of specialists in plant diseases. University students, however, may be well aware that behind the established facts presented here many unsolved questions still arise.

The author's hope will certainly be fulfilled: without doubt his book will become a substitute for the late Professor Thung's "Grondbeginselen der Plantevirologie", edited in 1949 and since long out of print.

We may congratulate the author as well as the Dutch students with the appearance of this modern introduction written in their own language. May they use it frequently!

L. C. P. Kerling

Kurt Hueck, Die Wälder Südamerikas, Ökologie, Zusammensetzung und wirtschaftliche Bedeutung. Gustav Fischer Verlag, Stuttgart. 1966, 422 pp., 253 afl. DM 72.— (geb.). (Vegetationsmonographien der einzelnen Grossräume, herausgegeben von W. Walter), Bd. 2.

In dit boek behandelt de auteur achtereenvolgens de volgende bosgebieden. Eerst de door hem onderscheiden 34 bosgebieden van het noordelijke gedeelte, de tropen, waarop volgen 6 bosgebieden van het zuiden, de subtropen en het gematigde gebied. Als aanhangsel volgt dan nog een korte behandeling van 9 bosloze en bosarme gebieden. Elk van die 40 hoofdstukjes worden – met kleine afwijkingen – ingedeeld in 5 paragrafen, te weten: 1, algemene opmerkingen,

2, hoofdvegetatietypen, 3, samenstelling, 4, economisch belangrijke houtsoorten, 5, exploitatie van het bos.

Hoewel deze indeling op zichzelf wel bruikbaar is, zijn er toch een aantal bezwaren. Het blijft n.l. een verzameling van grotendeels los van elkaar staande verhandelingen. Men wordt – behalve incidenteel – niet op weg geholpen naar een algemeen overzicht, naar de samenhang. Hiermee komen we gelijk aan het belangrijkste gebrek van dit boek: het is geen geheel en een synthese zoekt men vergeefs. Op enkele uitzonderingen na wordt nooit vergelijkend gewerkt. Noch vegetatiekundig, noch plantengeografisch zit er een lijn in. Aan de in de ondertitel genoemde oekologie komt de schrijver zelden toe, althans de vermelding van een paar cijfers over de regenval kan men bezwaarlijk oekologie noemen. Wat dat betreft kan men veel meer vinden in The Tropical Rainforest van Richards.

Een ander bezwaar is het gebrek aan evenwicht in de behandeling, een gebrek dat gedeeltelijk veroorzaakt wordt doordat het betreffende gebied nog maar weinig bestudeerd is, maar ten dele toch ook door het te weinig geinformeerd zijn van de schrijver. Zodra ik het boek in handen kreeg, heb ik natuurlijk het hoofdstuk Guiana opgeslagen. Dat werd een teleurstelling. Het oordeel zou moeten luiden: fragmentarisch, gedeeltelijk onjuist en gebrek aan literatuurkennis. Gelukkig is het voor het gehele boek niet zo erg. Er zijn gebieden, die er niet veel beter afkomen, maar er zijn ook gebieden die een veel betere behandeling hebben gekregen en die men zonder meer goed kan noemen. Zo bijv. het Zd. Braziliaanse Araucariabos. Allerlei aspecten van dit bostype worden uitvoerig behandeld. De samenstelling, de ontwikkeling en de gevaren die dit bos bedreigen worden uitstekend beschreven. Hier wordt ook nader ingegaan op algemene plantengeografische problemen. Men bemerkt duidelijk dat hier de auteur over eigen ervaring beschikte. Eerlijkheidshalve moet gezegd worden dat de schrijver, die midden vorig jaar is overleden, zelf deze heterogeniteit vermeldt in zijn voorrede. Het blijft echter jammer, dat de schrijver niet een andere opzet voor het boek heeft gekozen. Zou hij zich bijv. beperkt hebben tot die gebieden waar hij deskundig was en dan de gegevens uit de literatuur van de andere delen alleen gebruikt hebben voor een samenvatting, dan zou m.i. het boek aan waarde hebben gewonnen.

De foto's zijn over het algemeen goed en vormen als zodanig dan ook een waardevolle bijdrage. Het zijn grotendeels opnamen van de schrijver zelf. De tekeningen zijn soms illustratief, maar vrij vaak ook schetsmatig zó dat men er weinig aan heeft. Als naslagwerk, dus min of meer als een encyclopaedie heeft het werk zeker zijn waarde. Voor het opzoeken van de belangrijkste houtsoorten en het begruik van het bos lijkt het mij te onvolledig en te onpractisch gerangschikt om van waarde te zijn.

Ondanks de vele bezwaren zal toch in elke bibliotheek, die enigermate in deze richting is gespecialiseerd, het werk aanwezig dienen te zijn. Het is zeker weer een hulpmiddel om bepaalde gegevens te vinden.

J. Lanjouw

H. Buhr, Bestimmungstabellen der Gallen (Zoo- und Phytocecidien) an Pflanzen-Mittel- und Nordeuropas. Gustav Fischer Verlag, Jena. Bd. I, Pflanzengattungen A-M, Gallennummern 1–4388, 1964, XVI + 761 Seiten, DM 81,60. Bd. II, Pflanzengattungen N-Z, Gallennummern 4389–7666, 443 Figuren auf 25 Tafeln, 1965, 809 Seiten, DM 84,50.

Na de nog altijd belangrijke samenvattende gallenhandboeken voor grotere delen van Europa, n.l. HOUARD (1908–1913), RUEBSAAMEN (1911–1939, echter nooit voltooid) en ROSS and HEDICKE (1927) is er buiten ons land nooit meer een belangrijk determineerwerk voor de gallen van een streek van Europa verschenen. Nederland maakt hierop een zeer gunstige uitzondering met het Gallenboek van DOCTERS VAN LEEUWEN, waarvan de eerste druk in 1946 en de tweede in 1957 verscheen. Hoewel dit werkje 1257 verschillende gallen behandelt, is de bruikbaarheid van het boek buiten Nederland betrekkelijk gering. De andere bovengenoemde werken zijn reeds lang uitverkocht en ook antiquarisch niet of zeer moeilijk (en dan tegen hoge prijs) te verkrijgen.

BUHR heeft met deze twee lijvige delen dan ook in een behoefte voorzien. Het boek is het resultaat van 40 jaren studie van gallen, zowel die door dieren als door planten veroorzaakt. Zoals meestal gebruikelijk zijn ze gerangschikt naar de gastheerplant (genera); ook gallen op Cryptogamen zijn in het boek opgenomen. De inleiding tot deze tabellen is slechts kort. In 35 pagina's wordt een en ander uiteengezet over de biologie van de gallen en de cecidogene organismen, waarbij uit de verschillende onderdelen de moeilijkheden (bijv. om uit te maken wie de veroorzaker van een bepaalde gal is) zeer goed tot uitdrukking komen. Ook het bewaren van gallen en hun veroorzakers komt aan de orde. Omdat de gastheerplanten alfabetisch gerangschikt zijn, geeft de schrijver eerst een systematisch overzicht over deze planten. Naar mijn mening had dit achterwege kunnen blijven; het doet niet ter zake en men kan het in alle systematische handboeken vinden. Daarna volgen dergelijke systematische overzichten met commentaar over de cecidogene planten en dieren. Uit deze totaal 66 pagina's tellende inleiding blijkt wel de grondige kennis van de literatuur van de schrijver.

Het speciale deel, dat 1500 pagina's omvat, begint met een korte inleiding tot het gebruik van de tabellen en de afkortingen. De tabellen zijn in tegenstelling tot de oudere handboeken, vrijwel geheel dichotoom. Een bezwaar vindt recensent dat bij de eerste van de twee te maken keuzen verwezen wordt naar een hoger nummer in de tabel dan het nummer waarnaar de tweede keuze verwijst. Aangezien BUHR dit echter consequent doet, went men er vrij spoedig aan.

De gallen zijn in de tabel kort beschreven. In deze beschrijving staan ook van het genus de plantensoorten, waarop de gal tot nu toe is aangetroffen, opgesomd. Met kleine letter wordt dan verwezen naar de betreffende nummers in de drie belangrijkste boeken, die sterk afgekort zijn weergegeven. Ook hierbij komt wel het belang van ons Gallenboek van DOCTERS VAN LEEUWEN tot uiting; alleen HOUARD, ROSS-HEDICKE en DOCTERS VAN LEEUWEN zijn met enkele letters afgekort. De overige literatuur wordt met auteur(s) en jaartal vermeld. In de kleine letters vinden we ook aanduidingen over de biologie van de betreffende soort, synonymie, de verspreiding in Europa, e.d. (de landen ziin afgekort volgens de internationale kentekens voor motorvoertuigen). Het begrip gal is zeer ruim genomen. Alle Fungi, die maar enigszins vervormingen of uitwassen e.d. veroorzaken zijn opgenomen. De moeilijkheid daarbij is dat diverse op één plantensoort parasiterende Fungi, bijv. roesten, hetzelfde galbeeld veroorzaken. Deze soorten worden dan ook onder één punt achtereenvolgens opgesomd (hier is de tabel dus niet dichotoom) en men zal met een mycologisch werk nader de schimmelsoort moeten bepalen.

Na de laatste tabel volgen nog enige aanvullingen en verbeteringen, een lijst van afkortingen van auteursnamen, een uitvoerig register van de cecidogene organismen op genus- èn op triviaalnaam (90 pag.!) en de literatuurlijst (ook al 90 pagina's met naar schatting een 2700 literatuuropgaven). Alleen de literatuur van de laatste 30–40 jaar is verwerkt, op enkele noodzakelijke uitzonderingen na; de oudere literatuur vindt men in de oude handboeken. Het boek besluit met 25 pagina's afbeeldingen, waarop circa 350 soorten gallen staan afgebeeld. Er zijn slechts enkele originele tekeningen bij: de meeste zijn uit Ross, enkele uit DOCTERS VAN LEEUWEN, RUEBSAAMEN en anderen. Het is zeer te betreuren dat niet veel meer afbeeldingen zijn opgenomen. Op een totaal van 7666 soorten is 350 niet veel en de korte beschrijvingen maken het soms moeilijk een gal met zekerheid te determineren. Zonder ernstige prijsverhoging zou het opnemen van veel meer originele afbeeldingen de bruikbaarheid sterk vergroot hebben.

Een voornamelijk uit determineertabellen bestaand boek laat zich pas goed beoordelen door het gebruik. Recensent heeft een twintigtal hem onbekende, op verschillende gastheerplanten en in diverse landen verzamelde gallen met het nieuwe boek gedetermineerd. In het algemeen ging de determinatie vlot. Zelfs enkele gallen ver buiten het gebied, dat het boek bestrijkt en op planten, die ook niet in dit gebied voorkomen, konden dank zij de zeer volledige verwijzingen met behulp van andere literatuur toch gevonden worden. In een aantal tabellen moet men (evenals in andere gallenboeken) een keuze maken tussen de mogelijke veroorzakers van de betreffende gal. Hoewel in de inleiding hierover enige aanwijzingen worden gegeven, valt het niet altijd mee om de juiste keuze te bepalen. Voorts viel het recensent op dat *Psylla buxi*, een bladgal die op *Buxus sempervirens* overal zeer algemeen voorkomt, alleen te vinden is als men kiest: 'An Knospen oder Triebspitzen', terwijl 'An Blättern' niet tot het goede resultaat leidt. Weliswaar zitten de aangetaste bladeren aan de takken dicht opeen, doch de gal uit zich in de lepelvormig gekromde bladeren.

Afgezien van deze en mogelijke andere kleine onvolkomenheden is het boek een bijzonder welkome en ongewoon volledige aanwinst voor de gallenliteratuur. De boeken zijn in een fraaie linnen band gebonden. Er staan gezien de grote omvang opvallend weinig drukfouten in. De kwaliteit van het papier had beter gekund, doch komt het gewicht van de dikke delen wel ten goede. De prijs is, gezien de bijzonder overzichtelijke en toch vrij gecompliceerde typografie beslist niet uitzonderlijk hoog te noemen.

P. A. FLORSCHÜTZ

The Mineral Nutrition of the Rice Plant. Proceedings of a Symposium at the International Rice Research Institute, February, 1964. Published by the John Hopkins Press, Baltimore, Maryland, U.S.A., 1964. With many figures and tables.

When perusing a book like this, I can hardly suppress a feeling of jealousy. Times have changed since World War II, indeed! The investigator who in former years occupied himself with the physiology of rice, or, more general, with rice, had to find his own way in the immense field of rice literature. Papers on rice which were concerned with this crop were to be found in all kinds of scientific journals, either in a direct or in a more or less indirect way. Furthermore, important material on rice was accumulated in the Annual Reports from various Experimental Stations. In Japan an enormous number of papers on rice saw the light, for a great deal in Japanese, at best with an English or German summary. In the United States much was written on rice, but many papers were of only local importance.

Indo-China had its papers in French, the former Dutch East-Indies published in Dutch, Italy wrote in Italian and, not to mention more, the former British-India in English. Remembering those days one cannot help to be reminded of the famous words with which the book Judges closes: 'In those days there was no king in Israel, and everyone did exactly as he pleased'.

A situation like this was the more intolerable because rice is, both morphologically and physiologically, an extremely polymorphous crop withdifference problems under different circumstances. Already before the last war attempts were made to discuss these problems from a more general viewpoint, but important as rice may be, especially for the nutrition of Asia's millions, these attempts never resulted in the establishment of a central institute able to give guidance to the work on rice in the various (colonial) countries. Maybe the time was not yet ripe for such an institute – in our opinion this is hardly an excuse.

Anyhow, times have altered and what was deemed to be impossible before the war because of so many clashing interests, became reality after the cessation of hostilities. The Ford and Rockefeller Foundations, with the cooperation of the Government of the Philippines, established the International Rice Research Institute in Los Baños, Philippines. A central point, where investigations are carried on with respect to the manifold problems of rice and rice cultivation, especially in East- and Southeast-Asia, was a matter of fact!

It was this Institute that organized a Symposium on 'The Mineral Nutrition of the Rice Plant' in February 1964, and the book mentioned above contains papers from that Symposium and reports of the discussion that were held. In Session I the absorption, translocation and functions of nutrient elements are discussed. Session II deals with the nutrient requirements at different stages of growth. In Session III an analysis is given of the nutrient requirements of the rice plant in relation to supply. A review of the varietal characters and fertilizer responses is the subject of the Session IV and in Session V the whole Symposium is summarized.

Of the 29 participants (there were far more observers) 14 came from Japan and 8 from the Philippines – so the character of this congress was somewhat one-sided. No one came from India, Indonesia and Malaya – so one need not wonder that the subject of this Symposium was not exhausted and that not every aspect of the mineral nutrition of the rice plant came to the fore.

Nevertheless, a book like this needs to be welcomed heartily. It furnishes a basis to future workers in the mineral nutrition of the rice plant. And it is hoped to be a stimulus to all those who wish to enlist themselves in the great army of fighters against world's mightiest enemy: hunger. To all those . . . biologists not in the last place.

L. W. KUILMAN

J. LANJOUW, R. VAN DER WIJK, L. ANKER, O. H. BLAUW, V. J. KONINGSBERGER, M. J. SIRKS, H. J. LAM en V. WESTHOFF, Uit de plantenwereld. Uitgeversmaatschappij W. de Haan N.V., Zeist; Van Loghum Slaterus' Uitgeversmaatschappij N.V., Arhem; N.V. Standaard Boekhandel, Antwerpen. 1965. 375 blz.

Dit boek is, aldus de uitgevers tegenover de inhoudsopgave, een sterk gewijzigde en vernieuwde editie van HET LEVEN DER PLANTEN, onder redactie van

Prof. Dr Th. Weevers, verschenen in 1939 (tweede druk 1943) bij W. de Haan te Zeist.

De tweede druk van Weevers' boek heb ik nooit gezien, vermoedelijk omdat ik bij zijn verschijning op een ander deel van onze aarde wat in mijn bewegingen werd beperkt. De eerste druk ken ik wel en die staat nog altijd als een monumentaal boekwerk in mijn bibliotheek, alleen al om daarmee mijn leermeester en promotor te eren. Wat nu als een sterk gewijzigde en vernieuwde editie wordt geboden, is geen monumentaal boek meer, maar een soort dubbele pocket, die bij veelvuldig gebruik wel spoedig uit de band zal liggen. Naar het uiterlijk is de verwantschap tussen „Het leven der planten" en „Uit de plantenwereld" ver te zoeken. Naar het innerlijk daarentegen is die verwantschap groter. Het boek van Weevers werd destijds geschreven voor hen, die middelbaar onderwijs hebben genoten en wilde (uiteraard) tegelijkertijd wetenschappelijk verantwoord zijn. In „Uit de plantenwereld" „geven de auteurs een verantwoording van hun vakgebied, waarbij ze echter geen ‚vaktaal' spreken maar zich mede richten tot een algemene lezerskring van geïnteresseerden".

Een wat breder omschrijving van het doel, dat uitgevers en schrijvers bij de samenstelling van dit werk voor ogen stond, zou mijns inziens geen overbodige weelde zijn geweest. Want de vraag, die mij bij het lezen en herlezen van dit boek besloop en waarmee ik ben blijven zitten, is nu juist die van het doel, dat allen, die bij de uitgifte van dit boek zijn betrokken, daarmee hebben gehad. De schrijvers spreken geen vaktaal, zeggen de uitgevers op de omslag. 't Is maar wat je vaktaal noemt! Naar mijn smaak is, om een voorbeeld te noemen, de wijze, waarop in dit boek de indeling van het plantenrijk wordt behandeld, voor het overgrote deel alleen maar van betekenis voor de mensen van het vak, die . . . deze uiteenzetting niet nodig hebben. Ik kijk bijvoorbeeld naar figuur 19, waarin de zaadknop van *Pinus* wordt afgebeeld. Het figuurtje is omgeven door vijf woorden: micropyle, integument, nucellus, secundair endosperm, en macroprothallium. Een ander voorbeeld uit hetzelfde hoofdstuk. Ik lees: „Bij de meeste Phaeophyten komt een echte generatiewisseling voor waarbij een diploïde sporofyt afwisselt met een haploïde gametofyt". In een hoofdstuk „Onderwerpen uit de biochemie" vind ik een lijst van 13 groepen van enzymen, keurig met hun wetenschappelijke naam en achter die naam een omschrijving van het gekatalyseerde reactietype. In datzelfde hoofdstuk treft men vele bladzijden met scheikundige formules aan. Men wordt voorts in dit boek ingelicht over fototropie en geotropie, maar thermotropie, hydrotropie, galvanotropie en thigmotropie worden echt niet vergeten. De nutaties en nastieën krijgen ook hun beurt en voor wie het laatste wat oppervlakkig mocht vinden: epinastie, hyponastie, fotonastie, thermonastie, nyctinastie en seismonastie staan er alle in. Bij de plantengeografie vindt men bladzijden vol met een uiterst summiere beschrijving van allerlei vegetaties en worden onder het hoofd „Floristische plantengeografie" behandeld: A. de historische plantengeografie, en B. de statistische epiontologie. Op de bladzijden 305, 306 en 307 staan de verschillende formaties in een groot schema afgedrukt en op bladzijde 330 kan de algemene lezerskring van geïnteresseerden de schema's vinden van enkele successies in vaktaal-tot-en-met.

Het is er verre van, dat ik één van de schrijvers of uitgevers onaangenaam wil zijn, maar de vraag blijft: wat willen zij met dit boekske? Een groter publiek liefde, of op zijn minst belangstelling voor de planten bijbrengen? Het spijt mij, dat ik het moet zeggen — daarin hebben zij ten enen male gefaald. Daarvoor staan zij in dit werk veel te veel in en om de academische katheder en veel te weinig tussen de mensen tot wie zij willen spreken. Die mensen, intellectuelen of niet, willen best, ja graag! horen over planten. Maar dan moet hun worden verteld, gewezen, getoond — dan moeten zij worden meegenomen om te luisteren, erbij stil te staan, zich te verwonderen . . . Maar dan moet men niet bij hen komen met een onberispelijke opsomming, waarin geen onvertogen woord staat en waarin geen oneffenheden te bespeuren vallen. Heimans en Thijsse hebben toch niet tevergeefs geleefd?

L. W. Kuilman

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*) Not listed are the generic and specific names of the papers by Ross (p. 147–161); Vermeulen (p. 224–258); and de Smidt (p. 630–647).

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